

Reproductive failure predicts intracolony dispersal of female black-tailed prairie dogs (*Cynomys ludovicianus*) in a northern population

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ABSTRACT.—Dispersal in mammals is typically male-biased and occurs primarily in sexually immature individuals. These dispersal characteristics are especially true for ground-dwelling sciurids, such as black-tailed prairie dogs (*Cynomys ludovicianus*), that have polygynous breeding systems, with dispersing males and philopatric females. Prairie dogs are small, colonial rodents found in patches throughout the Great Plains of North America. Previous literature reports that females exist in philopatric units called coteries, typically with one unrelated breeding male. Yearling males disperse from their natal coterie in order to form their own coteries. We observed 1450 prairie dogs over 3 consecutive years in one colony near the northern limit of this species' range, in Grasslands National Park, Saskatchewan. We found that female dispersal occurred at higher rates than previously reported in the literature. We found no difference between the rate of intracolony dispersal for males and females in our study population. Also, we observed that the majority (14/21) of the dispersing females had recently experienced reproductive failure. We suggest that these females dispersed to increase their potential fitness by attempting reproduction in a new territory. This finding is the first instance of a ground-dwelling sciurid demonstrating female-biased breeding dispersal and suggests that factors influencing dispersal are more complicated than previously reported for black-tailed prairie dogs.

RESUMEN.—La dispersión en los mamíferos típicamente es parcial a los machos, y ocurre principalmente en individuos sexualmente inmaduros. Esto es especialmente cierto para las ardillas que viven debajo del suelo, por ejemplo, los perritos de las praderas de cola negra (*Cynomys ludovicianus*), que tienen sistemas de reproducción poligínicos con machos que dispersan y hembras que permanecen filopáticas. El perrito de las praderas de cola negra están roedores pequeños y colonial que vive en parcelas a lo largo de las Grandes Llanuras de América del Norte. La literatura reporta que las hembras existen en grupos filopáticos que se llaman coterías, típicamente con un macho reproductor no emparentado. Los machos añejos dispersan del coterie natal para establecer nuevos coterías. Observábamos 1450 perritos de la pradera a través de tres años consecutivos en 1 colonia a cerca del límite norteño del rango de esta especie en El Parque Nacional de Grasslands. Encontramos que dispersión de las hembras ocurre en una proporción más grande de lo que ha sido reportado anteriormente. No encontramos diferencias entre la proporción de dispersión intracolonia entre machos ni hembras en nuestra población de estudio. Además, observamos que la mayoría (14/21) de las hembras que dispersaron fallaron a reproducir recientemente. Sugerimos que estas hembras dispersaron a mejorar su capacidad por intentando a reproducir en territorio nuevo. Este es la primera ejemplo de un sciurido que habita a dentro del suelo demostrando una dispersión reproductiva sesgada por las hembras y sugiere que las razones por dispersión están más complicadas que ha sido reportan en el pasado para los perrito de las praderas de cola negra.

Dispersal is a well-documented aspect of an organism's life cycle, particularly in birds and mammals, happening when an individual moves permanently from one geographic area to another often for the purpose of reproduction (Greenwood 1980, Dobson 1982). Dispersal promotes genetic exchange within a species, and is therefore regarded as a highly important aspect of an organism's life cycle (for a review, see Clobert et al. 2012). Dispersal is

often classified into 2 types: natal and breeding. Natal dispersal describes when an individual moves from their natal territory before their first reproductive event, and breeding dispersal describes when an individual moves between 2 successive reproductive events (Johst and Brandl 1999). While costs are associated with dispersal (Bonte et al. 2012), they are assumed to be offset by a number of benefits. Increased mate choice, inbreeding avoidance,

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and decreased resource competition are 3 primary benefits to dispersal from a natal group (Greenwood 1980, Dobson 1982, Favre et al. 1997, Lukas and Clutton-Brock 2011, Armitage et al. 2011). Sex-biased dispersal patterns are well documented, with males typically acting as the dispersers in mammalian species, especially in polygynous breeding systems (Greenwood 1980, Dobson 1982, 2013).

However, documentation of female dispersal in a number of mammalian species is available and suggests that such dispersal may be more common than traditionally reported (Wrangham 1980, Pusey 1987, Clutton-Brock 1989, Price and Boutin 1993, Perry et al. 2008, Lukas and Clutton-Brock 2011; see Lawson Handley and Perrin 2007 for a review). In these instances, several sources proposed benefits to females, including (1) the bequeathal of a territory to offspring by mothers (Price and Boutin 1993), (2) the avoidance of inbreeding with male kin that still hold breeding tenure within the female's natal territory (Clutton-Brock 1989, Lukas and Clutton-Brock 2011), (3) the improvement of cooperation (in the case of parallel dispersal [Romano et al. 2019] or lack of cooperation at the natal territory [Armitage et al. 2011, Dobson 2013]), and (4) the heterogeneous distribution pattern of resources such that competition is elevated in the natal territory (Wrangham 1980, Favre et al. 1997). Despite the variety of potential benefits of female dispersal, overwhelming literature supports the notion that male-biased dispersal is substantially more common in mammalian species. To further this point, in their discussion of sex-biased dispersal, Devillard and colleagues performed a comprehensive meta-analysis for natal dispersal in ground-dwelling sciurids, furthering the support for male-biased dispersal in socially complex polygynous systems (Devillard et al. 2004).

The black-tailed prairie dog (*Cynomys ludovicianus*) is a social species that reportedly avoids inbreeding through male dispersal and female philopatry (Hoogland 1982, 1995). Prairie dogs aggregate in groups called coterie, which generally consist of one breeding male, several breeding females, and yearlings and juveniles of both sexes (Hoogland 1995). Males typically disperse prior to sexual maturity (e.g., natal dispersal; Halpin 1987). Alternatively, they may also disperse after sexual maturity for the purpose of reproduction

(breeding dispersal; Greenwood 1980). In both natal dispersal and breeding dispersal, these events may occur within and across colonies.

Several previous studies explore the prevalence of sex-biased dispersal in black-tailed prairie dogs, with some mention of female dispersal. This previous work reported a relatively even split between the sexes in inter-colony dispersal (56% males, $n = 34$; 44% females, $n = 27$) (Garrett and Franklin 1988). Intracolony dispersal, however, was dominated by males, with 90% of intracolony dispersers being male ($n = 36$) (Garrett and Franklin 1988). Of these dispersers, 83% were yearlings ($n = 30$), suggesting that a lack of available mates and an avoidance of inbreeding were the primary reasons for dispersing (Garrett and Franklin 1988). This study did not explore the factors driving female intracolony dispersal due to the small sample size ($n = 4$) (Garrett and Franklin 1988). Similarly, in a study on natal dispersal, all males ($n = 10$) dispersed from the natal coterie, while only one female dispersed (Halpin 1987). The authors were not able to document a reason for this female's dispersal nor the evidence for her success in a new location. Hoogland's (1995, 2013) long-term study of prairie dogs in Wind Cave National Park reported similarly low rates of female dispersal ($n = 11$) among 287 females tracked through their lifetime, with further observation that intracolony dispersal for females is extremely rare. The females of that population appear to follow a trend opposite that of males; philopatry is shown when the mother and siblings remain in the natal coterie (Hoogland 2013). Indeed, cooperation amongst kin is an important fitness determinant for many species (Axelrod and Hamilton 1981) and seems to explain why female prairie dogs may disperse from their natal territory in instances when the benefits of kin cooperation deteriorate or disappear. However, this explanation is only relevant for natal dispersal, as 8 of the 11 female dispersers were sexually immature (Hoogland 1995, 2013). These examples highlight the rarity of female dispersal in previously reported literature on this species and suggest avenues to explore potential causes for this dispersal.

Previous studies investigating female dispersal encountered limitations of small sample sizes and dispersals restricted to a single age class. Here, we provide broader evidence

for female dispersal in a northern population of black-tailed prairie dogs across a large sample that includes multiple age classes, and we explore the role of reproductive failure as a potential contributor to this dispersal.

METHODS

We made observations of intracolony dispersal across 3 years of an ongoing study (March–October 2015, March–August 2016, and March–August 2017) on a single black-tailed prairie dog colony in Grasslands National Park, Saskatchewan (49°3'47" N, 107°21'29" W). This colony varied in size over the course of the study (see results). Vegetation consisted of short-grass prairie dominated by blue grama grass (*Bouteloua gracilis*) and related graminoid species (Wiken 1986). We live-trapped (Tomahawk Live Trap, Tomahawk, WI) individual prairie dogs and, for first captures, marked them with a unique alphanumeric ear tag in each pinna (Monel #1, National Band and Tag Co., Newport, KY). We also marked their dorsal pelage with Nyanzol D dye (Greenville Colorants, Clifton, NJ) for individual identification. As the colony expanded, our trapping effort extended to new areas of the colony.

For all prairie dogs that we observed dispersing, we recorded pre- and postdispersal locations. We defined dispersal as any movement of a prairie dog from its natal coterie to a new geographic area farther than an adjacent coterie without return to the former coterie. We excluded any individuals that were observed only within their natal coterie or only intermittently beyond this territory. We determined the predispersal location by calculating the midpoint of activity for each individual based on its trapping locations in the natal coterie. For the postdispersal location, we calculated the midpoint of activity based on its trapping locations upon settling in a new location in the colony. Because prairie dogs live within coterie that average 50 m in diameter (Hoogland 1995), the dispersal distances we calculated could range ± 25 m from the distance listed in Table 1.

In order to examine the relationship between dispersal and previous breeding success, we monitored reproduction of all trapped females. From March to May of each study year, we live-trapped and palpated each female once

per week to monitor reproduction until parturition or abortion. We determined parturition through vulvar examinations (bloody, swollen, open), a large drop in mass (>50 g), and the presence of lactating teats (large, dark in color, swollen). We continued to trap lactating females once per week until juvenile emergence (expected 4–6 weeks after parturition; Hoogland 1995). We considered females who appeared to be pregnant based on palpation, but who never developed lactating teats to have aborted their litter before parturition. We considered females who abruptly stopped lactating prior to juvenile emergence to have lost their litter. Following juvenile emergence, we attributed juveniles to mothers using behavioral observations and known locations of nest burrows and juvenile activity.

We completed all analyses in R version 3.4.1 (R Development Core Team 2017). To explore dispersal differences between sexes, we used methods described in Hoogland (2013). We computed differences between sex and age using a 2×2 contingency table (chi-square test: $df = 1$). We also used this method to investigate dispersal differences between our study population and the one in Wind Cave National Park. We evaluated the effect of sex and age on dispersal distance with a 2-way analysis of variance (ANOVA), as our data were normally distributed. To determine if reproductive success impacted dispersal rates in females, we used a 2×2 contingency table (chi-square test: $df = 1$). We considered P values significant at $\alpha < 0.05$.

Our full data set included one group of individuals that dispersed together. We analyzed our data with this group included and with this group excluded and found the results to have equivalent statistical significance. Therefore, we present only the results for the entire data set, including the group dispersers.

RESULTS

Over the study period we live-trapped 1450 prairie dogs, of which 756 were female and 684 were male. We also observed the colony expanding from 60 ha to 120 ha during this period. Density varied spatially and temporally over the study period, ranging from approximately 8 adults/ha early in the sampling period to over 40 adults/ha in highly dense coterie. During the sampling period

TABLE 1. Black-tailed prairie dogs (*Cynomys ludovicianus*) that dispersed from their natal territory in one colony in Grasslands National Park from 2015 to 2017. The 7 individuals listed as dispersing in a group denote the composition of that specific group.

Individual	Dispersed alone or in a group	Dispersal distance (m)	Sex	Age
N dot	Alone	33	Female	Adult
UT	In a group	187	Female	Adult
ET	Alone	277	Female	Adult
dot P	Alone	301	Female	Adult
B dot	Alone	310	Female	Adult
JA	Alone	360	Female	Adult
RV	Alone	367	Female	Adult
:L:	Alone	480	Female	Adult
HM	Alone	521	Female	Adult
QL	Alone	28	Female	Yearling
Md	Alone	43	Female	Yearling
+N	Alone	127	Female	Yearling
F=	In a group	182	Female	Yearling
Xq	In a group	183	Female	Yearling
X:	In a group	183	Female	Yearling
Eq	In a group	183	Female	Yearling
E pi	In a group	184	Female	Yearling
dot R	Alone	202	Female	Yearling
bar H	Alone	286	Female	Yearling
JC	Alone	378	Female	Yearling
EE	Alone	604	Female	Yearling
VL	Alone	132	Male	Adult
d+	In a group	377	Male	Adult
RK	Alone	84	Male	Yearling
Od	Alone	104	Male	Yearling
=C	Alone	125	Male	Yearling
NT	Alone	145	Male	Yearling
IX	Alone	156	Male	Yearling
GB	Alone	160	Male	Yearling
dot N dot	Alone	167	Male	Yearling
ZV	Alone	184	Male	Yearling
GE	Alone	193	Male	Yearling
ZK	Alone	200	Male	Yearling
VT	Alone	202	Male	Yearling
U+	Alone	207	Male	Yearling
IE	Alone	212	Male	Yearling
BE	Alone	251	Male	Yearling
dot L dot	Alone	274	Male	Yearling
L?	Alone	301	Male	Yearling
L cent	Alone	483	Male	Yearling
ZW	Alone	547	Male	Yearling
EC	Alone	648	Male	Yearling
UN	Alone	1060	Male	Yearling

(2015–2017), we also observed high levels of reproduction: females produced an average of 4.08 ± 1.46 (mean \pm SE) juveniles per litter, while the 5-year average (2014–2018) within our entire data set was 3.06 ± 1.27 juveniles per litter.

We were able to track 170 females and 106 males of the animals we trapped for between 12 and 24 months to determine if they dispersed or remained philopatric. Of those tracked, 233 (84.4%) were philopatric and 43 (15.6%) were dispersed (natal or breeding).

When we analyzed the data for adults and yearlings together, there were no difference in dispersal rate between males (22/106) and females (21/170) ($\chi^2 = 2.89$, $P = 0.09$). When we separated the animals by age classes, there was a difference between sexes for yearlings ($n = 224$, $\chi^2 = 5.52$, $P = 0.02$) but not for adults ($n = 52$, $\chi^2 = 0.001$, $P = 0.98$) for rates of dispersal (Fig. 1); male yearlings (20/94) were more likely to disperse than female yearlings (12/130). When considering age groups within sex, we observed significant differences.

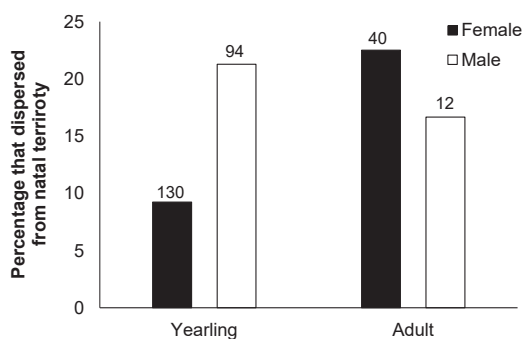


Fig. 1. Percentage of individuals that dispersed from the natal territory versus age at time of dispersal for black-tailed prairie dogs (*Cynomys ludovicianus*) in Grasslands National Park from 2015 to 2017. Numbers above each bar indicate the total number of individuals in each category.

For males, dispersal was not significantly different between yearlings and adults ($n = 106$, $\chi^2 = 5.84 \times 10^{-30}$, $P = 0.99$). For females, adults (9/40) were significantly more likely to disperse than yearlings (12/130) ($n = 170$, $\chi^2 = 3.82$, $P = 0.05$).

In the Grasslands National Park study colony, we documented much higher rates of intracolony dispersal by females relative to previous studies. The literature reports that 73% to 90% of dispersal is by males (Hoogland 1995, 2013, Garrett and Franklin 1988, Halpin 1987), while our results suggest that males were responsible for 51% of the dispersal events. We compared the 43 dispersal events at our study site with 2 studies from the Wind Cave National Park site (Garrett and Franklin 1988, Hoogland 2013) that presented similar sample sizes of 36 and 43 dispersers, respectively. We observed 22 male dispersers, while the Wind Cave studies observed 32 and 32, respectively. We observed a significant difference between these 2 study sites (Garrett and Franklin: $n = 79$, $\chi^2 = 11.21$, $P > 0.01$; Hoogland: $n = 86$, $\chi^2 = 4.03$, $P = 0.04$): female prairie dogs in our study site were significantly more likely to disperse than those in the study populations in Wind Cave National Park.

Among females, dispersal was closely linked with the success of the previous reproduction attempt (Fig. 2). We were able to track 61 females from pregnancy to parturition, with 40 litters emerging from their natal burrow. The majority of lost litters (16/21) occurred between parturition and juvenile emergence,

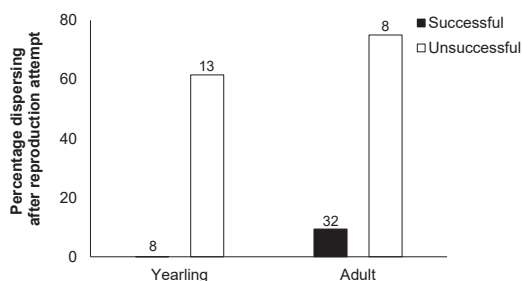


Fig. 2. Percentage of female black-tailed prairie dogs (*Cynomys ludovicianus*) that dispersed from the natal territory after a reproduction attempt in Grasslands National Park from 2015 to 2017. Numbers above each bar indicate the total number of individuals in each category.

with a small number occurring before parturition (5/21). There was an inverse relationship between reproductive success and dispersal in which females that had a litter survive to emergence were less likely to disperse for both adults ($n = 40$, $\chi^2 = 12.71$, $P < 0.01$) and yearlings ($n = 21$, $\chi^2 = 5.56$, $P = 0.02$). There was a similar pattern between adults and yearlings for dispersal based on litter loss. For adult females that lost a litter, 6/8 (75.0%) dispersed, while for yearling females that lost a litter, 8/13 (61.5%) dispersed; this difference was not significant ($n = 21$, $\chi^2 = 0.08$, $P = 0.77$). For those females that successfully reared a litter to emergence, only 3/32 (9.4%) adults dispersed and 0/8 (0.0%) yearlings dispersed ($n = 40$, $\chi^2 = 0.02$, $P = 0.89$). An additional 4 yearling females did not become pregnant and subsequently dispersed.

All of the dispersals occurred in the weeks following juvenile emergence. Both males and females departed from the natal burrow and moved to new territories in other parts of the colony. We rediscovered most of these individuals again near or on the edge of the existing colony ($n = 40$), but a small number ($n = 3$) moved one coterie over, which was located on the opposite side of a gravel road. We did not find these individuals on the natal side of the road at any point following the dispersal, indicating that true dispersal had occurred, albeit at a much shorter distance than those that dispersed to the edge of the colony. On average, adult female prairie dogs moved 315.11 ± 48.87 m and yearling females moved 215.25 ± 44.43 m. For males, dispersing adults moved 254.50 ± 112.50 m and yearlings moved 285.15 ± 52.58 m. The 2-way

ANOVA revealed no significant difference in the distance travelled between sexes ($n = 43$, $F_{1,32} = 0.02$, $P = 0.89$) or age groups ($n = 43$, $F_{1,32} = 0.19$, $P = 0.67$). The interaction between age and sex was also not significant ($n = 43$, $F_{1,32} = 1.01$, $P = 0.32$).

DISCUSSION

We explored the substantially higher rate of female dispersal in black-tailed prairie dogs observed in Grasslands National Park and investigated the relationship between reproductive failure and dispersal. Specifically, of the observed dispersing females, 14 experienced reproductive failure, 3 were reproductively successful, and 4 did not attempt reproduction. We described 4 potential explanations for female dispersal in our introduction: (1) maternal bequeathal, (2) avoidance of inbreeding, (3) increased opportunity for cooperation, and (4) decreased competition. We will explore which, if any, of these reasons help interpret the trend of female dispersal observed in our study population.

The first explanation (bequeathal of maternal territory to offspring) describes a mode of breeding dispersal that is uncommon among ground-dwelling sciurids (Dobson 1982, Hoogland 1995) and other mammals (Pusey 1987, Clutton-Brock and Lukas 2012). In this instance, a mother disperses from her territory following successful reproduction in order to bequeath this area to her offspring. Researchers have documented bequeathal in several other species (for a review, see Clarke et al. 2018), including Columbian ground squirrels (*Urocitellus columbianus*; Harris and Murie 1984) and North American red squirrels (*Tamiasciurus hudsonicus*; Price and Boutin 1993), both members of the Sciuridae. We observed this trend in 3 instances of dispersal in which adult females dispersed following the successful weaning of their litters. In 3 (14%) instances of female dispersal, young-of-the-year remained in the natal territory at the time of maternal dispersal, suggesting that there is some level of territory bequeathal among black-tailed prairie dogs. However, given that prairie dogs maintain group territories, the relationship between a female vacating her territory and the direct benefits for her offspring is difficult to untangle and may require further investigation.

The second explanation for female dispersal was avoidance of inbreeding by leaving a territory in which male kin are sexually mature (Clutton-Brock 1989, Lukas and Clutton-Brock 2011). We observed 4 sexually immature individuals move from their natal territory, suggesting that avoidance of inbreeding may be a factor. However, 3 of these 4 females dispersed as part of a larger group that included their mothers, leaving one (5%) individual that may have departed due to inbreeding avoidance. We do not have enough data to support avoidance of inbreeding as a factor driving this example of female dispersal, but we also cannot rule out the possibility.

We suggest that the third explanation (increased opportunity for cooperation) is a more suitable interpretation of the 3 sexually immature females that dispersed as part of a group. Because this dispersal occurred in a group, it can be considered parallel dispersal (Romano et al. 2019), during which individuals follow dispersing individuals to remain in close proximity to cooperative kin. Research on ground-dwelling sciurids supports the presence or absence of cooperative kin as a driver of philopatry or dispersal in several species (Viblanco et al. 2010, Armitage et al. 2011, Dobson 2013), including black-tailed prairie dogs (Hoogland 2013). In particular, Hoogland (2013) found that sexually immature prairie dogs are more likely to disperse when the mother or female kin have already dispersed. Our results suggest that this mechanism also occurs in our population because we observed it in 14% of our data.

The first 3 explanations of female dispersal presented in the literature can account for 33% of the female dispersal we observed. The remaining two-thirds of dispersing females experienced reproductive failure, which we suggest is the primary driver for female dispersal in this study population of black-tailed prairie dogs. As we discussed, most of these failures occurred after parturition but before juvenile emergence. This is the period during which females are in peak lactation and (as with other mammalian species) require increased resources because of the females' high energetic demands (Wade and Schneider 1992). We observed a dramatic increase in foraging to meet these energy demands (J. Kusch personal observation). We suggest that the females that experienced reproductive

failure were not able to acquire their needed resources primarily due to competition for those resources. As a result, these females dispersed from their home territory to improve their chances of successful reproduction in a new territory.

Furthermore, females did not disperse immediately after reproductive failure, but during the time of juvenile emergence. Typically, 80% of all dispersals within the species occur within this time period (Hoogland 1995), likely because the emergence of new juveniles causes a dramatic increase in density, further limiting food resources, and an increase in competition (Greenwood 1980). Demographic changes such as a dramatic shift in sex or age structure are known to be drivers of dispersal (Shields 1987). For example, there is evidence that a shift in age structure can increase the probability of dispersal in white-tailed deer (*Odocoileus virginianus*; Long et al. 2008). While we propose that reproductive failure is the primary driver of the dispersal of these 14 females from their home territory, we also acknowledge that reproductive failure is influenced by conspecific competition. As such, while the fourth explanation of dispersal (opportunity for decreased competition) is a contributor to the female dispersal we observed, we believe that reproductive failure is the more predominant influence.

Through the duration of our study, the population density of the colony increased. Within this time period, we observed a posid and female dispersal and found that the majority of dispersing females settled on or near the edge of the colony. Together, these events support the idea that some colony expansion can be attributed to breeding dispersal by female black-tailed prairie dogs. Typically, colony expansion is attributed to male dispersal (Hoogland 1995), but in this case, female intracolony dispersal may also contribute during periods of rapid population growth because densities across the colony were much higher. Overall, our observations suggest that during periods of increased population growth, female dispersal may be more frequent than previously reported and may be negatively correlated with reproductive success.

In conclusion, we find that a variety of factors influence female dispersal in black-tailed prairie dogs. Each of these influences relates

to animals attempting to maximize their fitness (both direct and indirect fitness) via different mechanisms. The mechanisms influencing female dispersal are more complicated than those traditionally described for males of the species, as is the role females play in contributing to the expansion of colonies. This raises the question of whether similar sex-based differences in dispersal influences and outcomes may be evident in other colonial species upon further investigation.

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LITERATURE CITED

- ARMITAGE, K.B., D.H. VAN VUREN, A. OZGUL, AND M.K. OLI. 2011. Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology* 92:218–227.
- AXELROD, R., AND W.D. HAMILTON. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- BONTE, D., H. VAN DYCK, J.M. BULLOCK, A. COULON, M. DELGADO, M. GIBBS, V. LEHOUCQ, E. MATTHYSEN, K. MUSTIN, M. SAASTAMOINEN, AND N. SHTICKZELLE. 2012. Costs of dispersal. *Biological Reviews* 87: 290–312.
- CLARKE, P.M.R., M.B. MCELREATH, B.J. BARRETT, K.E. MABRY, AND R. MCELREATH. 2018. The evolution of bequeathal in stable habitats. *Ecology and Evolution* 8:10594–10607.
- CLOBERT, J., M. BAGUETTE, T.G. BENTON, AND J.M. BULLOCK. 2012. *Dispersal ecology and evolution*. Oxford University Press, Oxford, UK. 462 pp.

- CLUTTON-BROCK, T.H. 1989. Female transfer and inbreeding avoidance in social mammals. *Nature* 337:70–72.
- CLUTTON-BROCK, T.H., AND D. LUKAS. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472–492.
- DEVILLARD, S., D. ALLAINE, J.M. GAILLARD, AND D. PONTIER. 2004. Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids. *Behavioral Ecology* 15:83–87.
- DOBSON, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.
- DOBSON, F.S. 2013. The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Animal Behaviour* 85:299–304.
- FAVRE, L., F. BALLOUX, J. GOUDET, AND N. PERRIN. 1997. Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London B* 264:127–132.
- GARRETT, M.G., AND W.L. FRANKLIN. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy* 69:236–250.
- GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- HALPIN, Z.T. 1987. Natal dispersal and the formation of new social groups in a newly established town of black-tailed prairie dogs (*Cynomys ludovicianus*). Pages 104–118 in D. Chepko-Sade and Z.T. Halpin, editors, *Mammalian dispersal patterns: the effects of social structure on population genetics*, B. University of Chicago Press, Chicago, IL.
- HARRIS, M., AND J. MURIE. 1984. Inheritance of nest sites in female Columbian ground squirrels. *Behavioural Ecology and Sociobiology* 15:97–102.
- HOOGLAND, J.L. 1982. *Prairie dogs avoid extreme inbreeding*. *Science* 215:1639–1641.
- HOOGLAND, J.L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press, Chicago, IL. 557 pp.
- HOOGLAND, J.L. 2013. *Prairie dogs disperse when all close kin have disappeared*. *Science* 339:1205–1207.
- JOHST, K., AND R. BRANDL. 1999. Natal versus breeding dispersal: evolution in a model system. *Evolutionary Ecology Research* 1:911–921.
- LAWSON HANDLEY, L.J., AND N. PERRIN. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- LONG, E.S., D.R. DIEFENBACH, C.S. ROSENBERY, AND B.D. WALLINGFORD. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. *Behavioural Ecology* 19:1235–1242.
- LUKAS, D., AND T.H. CLUTTON-BROCK. 2011. Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. *Journal of Evolutionary Biology* 24:2624–2630.
- PERRY, S., J.H. MANSON, I. MUNIZ, J. GROS-LOUIS, AND L. VIGILANT. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal Behavior* 76:187–199.
- PRICE, K., AND S. BOUTIN. 1993. Territorial bequeathal by red squirrel mothers. *Behavioral Ecology* 4:144–150.
- PUSEY, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2:295–299.
- R DEVELOPMENT CORE TEAM. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- ROMANO, V., A.F. MARTINS, AND C.R. RUIZ-MIRANDA. 2019. Unraveling the dispersal patterns and the social drivers of natal emigration of a cooperative breeding mammal, the golden lion tamarin. *American Journal of Primatology* 81(3):e22959. 13 pp.
- SHIELDS, W.M. 1987. Dispersal and mating systems: investigating their causal connection. Pages 3–24 in D. Chepko-Sade and Z.T. Halpin, editors, *Mammalian dispersal patterns: the effects of social structure on population genetics*, B. University of Chicago Press, Chicago, IL.
- VIBLANC, V.A., C.M. ARNAUD, F.S. DOBSON, AND J.O. MURIE. 2010. Kin selection in Columbian ground squirrels (*Urocitellus columbianus*) littermate kin provide individual fitness benefits. *Proceedings of the Royal Society B: Biological Sciences* 277:989–994.
- WADE, G.N., AND J.E. SCHNEIDER. 1992. Metabolic fuels and reproduction in female mammals. *Neuroscience and Biobehavioral Reviews* 16:235–272.
- WIKEN, E.B. 1986. *Terrestrial ecozones of Canada*. Environment Canada, Lands Directorate.
- WRANGHAM, R.W. 1980. An ecological model for female-bonded primate groups. *Behaviour* 75:262–300.

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