

THE INFLUENCE OF SITE FAMILIARITY AND KIN INTERACTIONS ON THE
DISPERSAL OF A PASSERINE BIRD

by

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A handwritten signature in black ink, appearing to read "Renée Duckworth", written over a horizontal line.

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ABSTRACT: Dispersal is a fundamental component of life history, but determining the causal factors behind individual dispersal decisions is often difficult. However, it is known that competitive and cooperative interactions can play an important role. Western bluebirds (*Sialia mexicana*) provide a unique opportunity to investigate the role of kin interactions mediated by aggressive behavior on local dispersal. A long-term dataset on relatedness, natal and breeding location, cavity density, and aggressive behavior was used to test the hypotheses. First-time breeding males dispersed non-randomly and settled closer than expected to their natal nest and father. Because fathers were frequently breeding at the natal nest, distance to both was strongly correlated. However, in cases where fathers did not return to breed, sons settled significantly closer to their natal nest suggesting that fathers may deter sons from settling as close to their natal territory as they would prefer. Although no significant role of aggression has yet to be found, there does appear to be some cooperation between kin over available cavity resources. These results support the importance of natal site familiarity and kin interactions in the local dispersal decisions of western bluebirds, but further studies are necessary to disentangle the relative importance of each.

KEYWORDS: natal dispersal, aggression, competition, cooperation, *Sialia mexicana*

INTRODUCTION:

Dispersal is a fundamental component of life history that influences the overall genetic and social composition of local populations (Hanski 1999, Clobert *et al.* 2001). Despite its importance, determining the causal factors behind individual dispersal decisions has been difficult. Social interactions, both cooperation and competition, have been implicated as drivers of dispersal. Dispersal may be promoted to avoid competition between kin (Strickland 1991) or fitness benefits may be gained by remaining philopatric and cooperating with kin (Jones *et al.* 1988, Wolff *et al.* 1988, Lambin and Krebs 1993). Moreover, resource availability can play an important role in determining whether cooperation or competition will occur in a given situation (Stacey and Ligeon 1987, Brown and Brown 1993). The balance between competitive and cooperative interactions plays a crucial role in dispersal decisions.

Social interactions between individuals can influence dispersal decisions (e.g. Beletsky and Orians 1989, Le Galliard *et al.* 2003, Cote and Clobert 2007, Vercken *et al.* 2012). Interactions with kin, specifically, can promote or discourage dispersal through fitness costs or benefits. For example, a benefit to both the offspring and parent occurs when philopatric young are tolerated by their parents (Jones *et al.* 1988, Wolff *et al.* 1988, Lambin and Krebs 1993). The offspring benefit from sharing resources with the parents, while the inclusive fitness of the parent's increases from the breeding success of the offspring. Cooperation between kin can also exceed simple tolerance between individuals. In European bee-eaters (*Merops apiaster*), for example, brothers that nest close to each other are more likely to help with the other's nest, should their own nest fail (Lessells *et al.* 1994).

When kin interact, there is a delicate balance between the benefits that are received by the offspring and the costs that are imposed upon the parents (Trivers 1974). If competition for

resources occurs between kin, dispersal may be promoted as a means to avoid the associated negative fitness costs (Ronce *et al.* 1998). A study of gray jays (*Perisoreus canadiensis*) found that competition between siblings resulted in the expulsion of one sibling (Strickland 1991). Related to competition for resources is population density, which has been shown to drive dispersal in a wide range of taxa, from invertebrates to mammals and birds (Berger 1992, Léna *et al.* 1998, Doak 2000, Doligez *et al.* 2004). Although both positive- (Massot *et al.* 1992) and negative-density dependent dispersal (Serrano *et al.* 2003, Stoen *et al.* 2006) are possible, positive-density dependent dispersal is related to competition for resources. When there is high competition with con- and heterospecifics, individuals may gain a fitness benefit by dispersing to less dense areas. The balance between kin cooperation and kin competition may be based on the availability of resources (Stacey and Ligeon 1987, Brown and Brown 1993). High resource availability may result in kin cooperation, while low resource availability may result in kin competition.

Aggressive behavior can be an important mediator of interactions between kin, as it is often used to defend resources (Garcia and Arroyo 2002, Brazill-Boast 2013) and influences dominance hierarchies between individuals (Dingemanse and de Goede 2004, Brazill-Boast 2013). Moreover, in many studies, aggression has been shown to be less intense between kin than between non-kin (Waldman 1988, Walls and Roudebush 1991, Pfennig *et al.* 1993, Watson *et al.* 1994). Thus, aggression can play an important role in determining if cooperation or competition between kin will be favored. Because aggressive behavior is less intense between kin, it is possible that this can lead to cooperation between kin and philopatry being favored. However, resource availability also has the potential to interact with aggression. If resources are

limiting, aggression may increase competitive interactions between kin or may necessitate cooperation between kin to attain the limited resources.

On the other hand, natal site familiarity can also influence dispersal decisions through a dispersal bias towards the natal site. Natal philopatry can be a beneficial strategy if familiarity allows individuals to better acquire necessary resources (Greenwood 1980, Krebs 1982, Pärt 1995). For instance, if territory acquisition is particularly difficult, being familiar with the site may provide a competitive advantage. Male blue tits (*Parus major*) have been shown to preferentially occupy their natal territory, if their father did not return to the natal site (Greenwood 1979). Moreover, it may be possible for individuals to predict the future quality of the natal site from their prior experience with it (Burger 1982, Blancher and Robertson 1985, Danchin *et al.* 1998). As dispersal is a very costly endeavor, individuals may be reluctant to disperse to an unknown area (Tenaza 1971). Thus, even if the natal site was not particularly high quality, an individual may choose to return rather than facing the potential costs of dispersing in search of an area of higher quality.

Western bluebirds provide a unique opportunity to investigate dispersal decisions. The study population in Montana consists of short-distance migrants with females that disperse away from the natal population and males that have variable dispersal behavior. Similar to non-migratory populations in California (Dickinson *et al.* 1996), facultative cooperative breeding occurs in Montana populations. At the population level, aggressive males possess a dispersing morph and tend to disperse out of their natal population, while nonaggressive males possess a philopatric dispersal morph and tend to remain in their natal population (Duckworth and Badyaev 2007). Aggressive males are better competitors for nest cavities (Duckworth 2006a), but invest little in parental care (Duckworth 2006b). Additionally, it has been shown that

nonaggressive males are more likely than aggressive males to nest adjacent to kin (Duckworth 2008). Previous work has focused on recently colonized populations with low breeding population density. It is not known if the links between aggression and dispersal remain once populations are settled.

In this study, I will use long-term data to investigate the dispersal of males from a well-established population where density of conspecifics is high. I will assess whether local (i.e. in site) dispersal decisions are random with respect to the natal nest and kin (fathers and brothers from the same clutch). Although it has been shown that nonaggressive males are more likely to nest adjacent to a relative and may benefit from budding off their parent's territory (Duckworth 2008), it is unclear if this clustering is a result of natal site familiarity (i.e. desire to be close to the natal nest) or a result of kin interactions (i.e. cooperation). If males are attracted to their natal nest or kin, the observed distance between the current breeding nest and the natal nest or kin will be smaller than the expected distance under a random settling pattern.

Aggressive behavior may have a direct influence on local dispersal through competitive and cooperative interactions between kin. Nest cavities are a vital resource and bluebirds tend to favor territories that have multiple cavities (Meek and Robertson 1994, Plissner and Gowaty 1995). If cooperation between kin is important, high resource density will increase the probability of sons breeding near fathers. On the other hand, if competition between kin is important, high resource density will decrease the probability of sons breeding near fathers (as fathers will not want to share the high resource territory). If aggression is an important mediator of kin interactions, there will be a positive relationship between aggression and dispersal distance, as nonaggressive males are more likely to cooperate and aggressive males more likely to compete.

METHODS:*Study site and general methods*

This study utilizes a long-term dataset from a nest box population of western bluebirds near Missoula, Montana (Figure 1). The site has been monitored for over a decade and a wealth of data on behavior, territory selection, and relatedness is available. During each field season, individuals are regularly observed to determine the affiliation of breeding pairs with specific nest boxes. Individuals are captured, sampled for DNA, and banded with a unique color combination.

Aggression is measured by simulating a territorial intrusion by a live tree swallow (*Tachycineta bicolor*), a heterospecific nest competitor. A tree swallow in a wire cage is placed on top of the nest box for two-minute trials. The number of times an individual attacked, flew by, or hovered near the cage is counted and a score of 1-6 is assigned (Duckworth 2006b). A score of 1 indicates a non-aggressive response, while a score of 6 indicates the most aggressive response. Measuring the response to tree swallows is meaningful in the context of territory acquisition and it has been shown that bluebirds are significantly more aggressive towards tree swallows than other non-cavity nesting species (Duckworth 2006b, Duckworth and Badyaev 2007).

Is dispersal of first-time breeders random with respect to the natal nest and kin?

I assessed whether first-time breeding males were settling randomly with respect to their natal nest and close kin (fathers and brothers from the same clutch). This study focuses on first-time breeders to avoid autocorrelation issues due to dispersal decisions made in successive breeding seasons. Sixty total first-time breeders between 2004 and 2012 were identified and of these, 15 did not have kin present on the study site during their first year of breeding. The 60

individuals were divided into three groups: those with no kin present, those with fathers present, and those with brothers present. If a male had both a father and brother present, he was randomly assigned to one of the two groups. Thus, each male appears only once in the statistical analysis to determine randomness of settling. To test whether males are attracted to or repelled from their natal site or kin, for all males, the distance between the male's current breeding location and natal nest and kin were determined using GoogleEarth.

To assess if males settled randomly with respect to the natal nest, the group of males with no kin present were used. In these males, the influence of the natal site is not confounded with the influence of kin, so it is possible to determine if males are attracted or repelled from the natal site independent from the potential influence of kin. The observed distances from each male's breeding nest to his natal nest was compared to an expected distance under the null hypothesis of random settlement. The expected distance was calculated as the average of all potential distances to the focal male's natal nest (e.g. the average distance to a male's natal nest from all potential breeding nests a male could have chosen). A similar method was employed to assess if males settled randomly with respect to their fathers or brothers by using the two remaining groupings (males with fathers present and males with brothers present). The expected distance in this case was calculated as the average of all potential distances to the focal male's kin, father or brother (e.g. the average distance to the father or brother from all potential nests a male could have chosen). Each observed distance was compared to the corresponding expected distance using a Wilcoxon signed-rank test.

Are cooperative or competitive interactions between kin driving local dispersal?

Bluebirds favor territories that have multiple nest cavities (Meek and Robertson 1994, Plissner and Gowaty 1995). Thus, the more nest boxes in a defendable territory, the higher quality the territory. The number of boxes within a 150 m radius circle around a focal box was used as a measure of resource quality. If cooperation between kin is important, high resource density will increase the probability of sons breeding near fathers. On the other hand, if competition between kin is important, high resource density will decrease the probability of sons breeding near fathers (as fathers will not want to share the resource). I evaluated the importance of this resource on dispersal decisions using a general linear model (GLM).

The integration of aggression and dispersal at the scale of the range expansion of the species would suggest that aggression might also play a role in more local dispersal decisions. To test the role of aggression, I assessed the influence of both focal male and father aggression on dispersal distance from the natal nest using a GLM. If aggression is an important mediator of kin interactions, there will be a positive relationship between aggression and dispersal distance, as nonaggressive males are more likely to cooperate and aggressive males more likely to compete.

RESULTS:

Is dispersal of first-time breeders random with respect to the natal nest and kin?

First-time breeding males settled non-randomly, settling closer than expected to their natal nest (Wilcoxon signed-rank test: $S = 44$, $P < 0.02$, $n = 15$; Table 1) and father (Wilcoxon signed-rank test: $S = 219$, $P < 0.001$, $n = 36$; Table 1) than would be expected under a random settling pattern. The distances to brothers did not differ significantly from a random settling pattern (Wilcoxon signed-rank test: $S = 13.5$, $P = 0.13$, $n = 9$; Table 1), but the sample size lacks

the power to detect a small effect. Fathers were frequently breeding at the natal nest, so the distance from a focal male to his natal nest and to his father was strongly correlated ($F = 295.42$, $P < 0.0001$, $n = 36$; Fig. 2). However, in cases where fathers did not return to the site, males settled significantly closer to the natal nest ($t = -2.50$, $P < 0.02$, $n = 51$; Fig. 3).

Are cooperative or competitive interactions between kin driving local dispersal?

The relationship between focal male aggression, natal box density, and distance dispersed was close to significant (GLM: $F = 2.28$, $P = 0.06$, $n = 63$). However, when aggression is not included in the model, the relationship between box density and distance dispersed is significant (GLM: $F = 3.76$, $P < 0.03$, $n = 63$). There was no significant relationship between focal male aggression, father aggression, and the distance to the natal nest using all males with fathers present (GLM: $F = 1.09$, $P = 0.35$, $n = 30$) or only males with fathers breeding at the natal nest (GLM: $F = 0.21$, $P = 0.81$, $n = 15$).

DISCUSSION:

Although dispersal is a fundamental component of life history, determining the causal factors behind individual dispersal decisions has been difficult. Both cooperative and competitive interactions have been implicated as drivers of dispersal (Jones *et al.* 1988, Wolff *et al.* 1988, Strickland 1991, Lambin and Krebs 1993), but familiarity to the natal site can be just as important (Greenwood 1980, Krebs 1982, Pärt 1995). Additionally, the availability of resources has the potential to play an important role in determining whether cooperation or competition will occur (Stacey and Ligeon 1987, Brown and Brown 1993).

First-time breeding male western bluebirds dispersed non-randomly and settled closer to their natal site and father than expected under a random settling pattern (Table 1). While this finding supports both natal site familiarity and cooperative interactions between kin as important determinants of dispersal, in cases where fathers were not present at the study site, sons settled significantly closer to their natal nest. This suggests that fathers may deter sons from settling as close to their natal nest as they would prefer. This latter result is opposite of what is expected under kin cooperation and instead suggests that competition between fathers and sons is important in local dispersal of western bluebirds. Because fathers are often breeding at the natal site, the non-random dispersal of males in relation to their father may simply result from a preference to be close to the natal territory. A similar result has been found in great tits (*Parus major*) and great cormorants (*Phalacrocorax carbo sinensis*). Great tit males are more likely to occupy their natal site if their father died in the previous year (Greenwood 1979), while great cormorants show dispersal that is biased towards the natal site and results in kin clustering around the natal nest (Schjørring 2001). Kin clustering is also apparent in this study, but it appears that the greater competitive ability of the father results in the son occupying a territory near the natal site, but rarely the natal site itself when the father is present.

The box density around the natal nest was negatively correlated with the dispersal distance, such that natal dispersal distance was smaller as box density increased (Fig. 4). This suggests that cooperation may occur around territories that possess higher box density. However, it is possible that higher box density independent of cooperative interactions could result in this pattern. If a bird breeds in a box adjacent to his natal box, it is only possible to be as close as the distance between the two boxes. If more boxes are close to the focal box, it is possible to disperse a shorter distance to be at an adjacent box than if the only nearby boxes are more

distant. Thus, it will be important to also address not just the presence of boxes around the natal nest, but also the availability of boxes (i.e. of the nearby boxes, how many are unoccupied). It is possible that other ecological resources, such as food availability, will also influence dispersal in this species. For instance, wing-dimorphic insects show different wing phenotypes depending on the population density and thus, competition for available resources (Denno *et al.* 1991). When the population density is high, the insects possess a dispersing phenotype to be able to disperse to an area that has the potential for more food (Denno *et al.* 1991). It is possible that local food availability will also be important in dispersal of western bluebirds. As insectivorous birds, the availability of insects around a box may be an important factor when choosing a nest box. It appears that box density plays an important role in dispersal decisions, but it is important to further study if this is a result of the simple presence of more boxes or of cooperative interactions between kin. Moreover, more information on local territory quality (e.g. food resources) will provide a better understanding of the interactions between kin over local resources.

Interestingly, aggression does not appear to influence dispersal decisions at this local scale. This is contrary to the integration of aggression and dispersal at the range expansion level (Duckworth and Badyaev 2007). It was expected that aggression and dispersal distance would be positively correlated, with aggressive males that disperse farther than less aggressive males. However, this does not appear to be the case at the local scale. This could result from focusing only on males that remain in their natal population to breed. Males that remain philopatric in their natal population, regardless of their aggression level, may disperse using a similar strategy. Thus, this may decouple aggression and dispersal at the local scale. Alternatively, previous work showing that nonaggressive males settled closer to kin also included mothers. Future studies will be investigating the role of mothers in local dispersal decisions, in a similar way that this study

looked at the role of fathers and brothers. Previous work was also on populations at the initial stages of colonization. An intriguing possibility is that the dynamics of kin interactions change during the course of population colonization in response to changing levels of resources and competition to obtain them.

Thus, it appears that natal site familiarity and competitive interactions between kin influence the local dispersal decisions of western bluebirds. It largely seems that males are driven to be as close to the natal territory as possible, but competitive interactions between fathers and sons often prevents sons from occupying the natal nest during their first year of breeding. Additionally, the availability of resources also influences local dispersal and this may be through cooperative interactions between kin, but needs further investigation. As a way to determine if cooperation between kin is occurring, future studies will address the home range sizes of males nesting adjacent and not adjacent to kin. If cooperation is occurring, males that nest near kin will be expected to have smaller home ranges than males that nest near non-kin. It will also be important to determine if any fitness benefits are gained from nesting near kin. Future studies will also focus on integrating mothers into the analyses and comparing the dispersal dynamics in the early stages of colonization to the dynamics in the later, more settled stages of colonization.

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LITERATURE CITED

- Beletsky, L.D. and G.H. Orians. 1989. Familiar neighbors enhance breeding success in birds. *Proceedings of the National Academy of Sciences of the USA* **86**: 7933-7936.
- Berger, A. 1992. Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bulletin of Entomological Research* **82**: 441-448.
- Blancher, P.J. and R.J. Roberston. 1985. Site consistency in kingbird breeding performance: implications for site fidelity. *Journal of Animal Ecology* **54**: 1017-1027.
- Brazill-Boast, J. 2013. Competition for resources mediated by intrinsic social dominance in sympatric finches. *IBIS* **155**: 189-193.
- Brown, G.E. and J.A. Brown. 1993. Do kin always make better neighbors? The effects of territory quality. *Behavioral Ecology and Sociobiology* **33**: 225-231.
- Burger, J. 1982. The role of reproductive success in colony-site selection and abandonment in black skimmers (*Rynchops niger*). *The Auk* **99**: 109-115.
- Clobert, J., E. Danchin, A.A. Dhont, and J.D. Nichols. 2001. *Dispersal*. Oxford University Press, Oxford.
- Colwell, R.K. and S. Naeem. 1999. Sexual sorting in hummingbird flower mites (Mesostigmata: Ascidae). *Annals of the Entomological Society of America* **92**: 952-959.
- Cote, J. and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B* **274**: 383-390.
- Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **79**: 2415-2428.
- Denno, R.F., G.K. Roderick, K.L. Olmstead, and H.G. Dobel. 1991. Density related-migration in planthoppers (homoptera, delphacidae) – the role of habitat persistence. *The American Naturalist* **138**: 1513-1541.
- Dickinson, J.L., W.D. Koenig, and F.A. Pitelka. 1996. Fitness consequences of helping behavior in the western bluebird. *Behavioral Ecology* **7**: 168-177.
- Dingemanse, N.J. and P. de Goede. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology* **15**: 1023-1030
- Doak, P. 2000. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology* **81**: 1828-1841.

- Doligez, B., T. Part, E. Danchin, J. Clobert, and L. Gustafsson. 2004. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* **73**: 75-87.
- Duckworth, R.A. 2006a. Aggressive behavior affects selection on morphology by influencing settlement patterns in a passerine bird. *Proceedings of the Royal Society B* **273**: 1789-1795.
- Duckworth, R.A. 2006b. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology* **17**: 1011-1019.
- Duckworth, R.A. 2008. Adaptive dispersal strategies and the dynamics of a range expansion. *The American Naturalist* **172**: S4-S17.
- Duckworth, R.A. and A.V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the USA* **104**: 15017-15022.
- Garcia, J.T. and B.E. Arroyo. 2002. Intra- and interspecific agonistic behavior in sympatric harriers during the breeding season. *Animal Behaviour* **64**: 77-84.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**:1140–1162.
- Greenwood, P.J., P.H. Harvey, and C.M. Perrins. 1979. The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *Journal of Animal Ecology* **48**: 123-142.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Jones, W., P. Waser, N. Elliott, N. Link, and B. Bush. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. *Ecology* **69**: 1466-1473.
- Krebs, J.R. 1982. Territorial defence in the great tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology* **11**: 185-194.
- Lambin, X., and C. Krebs. 1993. Influence of female relatedness on the demography of Townsend's vole populations in the spring. *Journal of Animal Ecology* **62**: 536-550.
- Le Galliard, J., R. Ferrière, and J. Clobert. 2003. Mother-offspring interactions affect natal dispersal in a lizard. *Proceedings of the Royal Society B* **270**: 1163-1169.
- Léna, J.P., J. Clobert, M. de Fraipont, J. Lecompte, and G. Guyot. 1998. The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology* **9**: 500-507.

- Lessells, C.M., M.I. Avery, and J.R. Krebs. 1994. Nonrandom dispersal of kin: why do European bee-eater (*Merops apiaster*) brothers nest close together? *Behavioral Ecology* **5**: 105-113.
- Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742-1756.
- Meek, S.B. and R.J. Robertson. 1994. Interspecific competition for nestboxes affects mate guarding in eastern bluebirds *Sialia sialis*. *Animal Behaviour* **47**: 295-302.
- Pärt, T. 1995. The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. *Animal Behaviour* **49**: 1029-1038.
- Pfennig, D.W., H.K. Reeve, and P.W. Sherman. 1993. Kin recognition and cannibalism in spadefoot toad tadpoles. *Animal Behaviour* **46**: 87-94.
- Plissner, J.H. and P.A. Gowaty. 1995. Eastern bluebirds are attracted to two-box nest sites. *Wilson Bulletin* **107**: 289-295.
- Ronce, O., J. Clobert, and M. Massot. 1998. Natal dispersal and senescence. *Proceedings of the National Academy of Sciences of the USA* **95**: 600-605.
- Schjørring, S. 2001. Ecologically determined natal philopatry within a colony of great cormorants. *Behavioral Ecology* **12**: 287-294.
- Serrano D. and J. Tella. 2003. Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of Animal Ecology* **72**: 400-410.
- Stacey, P.B. and J.D. Ligeon. 1987. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist* **130**: 654-676.
- Stoen, O.G., A. Zedrosser, S. Saebo, and J.E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* **148**: 356-364.
- Strickland, D. 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. *Canadian Journal Zoology* **69**: 2935-2945.
- Tenaza, R. 1971. Behaviour and nesting success relative to nest location in Adelie penguins (*Pygoscelis adeliae*). *Condor* **73**: 81-92.
- Trivers, R.L. 1974. Parent-offspring conflict. *American Zoologist* **14**: 249-264.

- Vercken, E., B. Sinervo, and J. Clobert. 2012. The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. *Behavioral Ecology* **23**: 1059-1067.
- Waldman, B. 1988. The ecology of kin recognition. *Annual Review of Ecology and Systematics* **19**: 543-571.
- Walls, S.C. and R.E. Roudebush. 1991. Reduced aggression toward siblings as evidence of kin recognition in cannibalistic salamanders. *The American Naturalist* **138**: 1027-1038.
- Watson, A., R. Moss, R. Parr, M.D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. *Journal of Animal Ecology* **63**: 39-50.
- Wolff, J.O., K. Lundy, and R. Baccus. 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. *Animal Behaviour* **36**: 456-465.

FIGURES

Figure 1. Study site in Missoula, MT. White circles represent nest boxes.

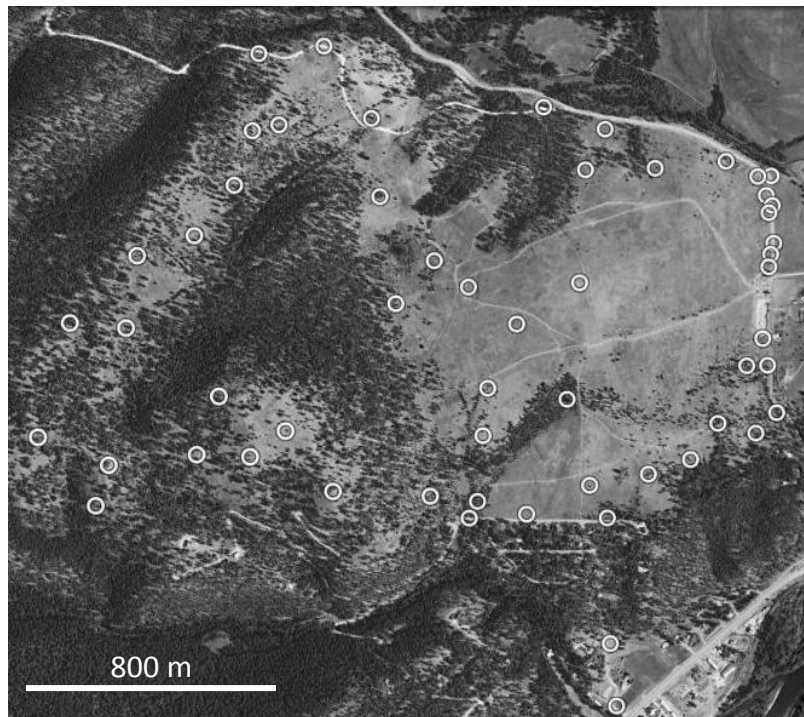


Table 1. Results to determine if first-time breeding males settle randomly with respect to their close kin (fathers and brothers) or natal nest.

Distance to	<i>n</i>	Average Observed Distance (m)	Average Expected Distance (m)	<i>p</i>
Fathers	36	720.7	1073.8	0.0002
Brothers	9	782.6	1131.7	0.1289
Natal Nest	15	451.7	936.9	0.0103

Figure 2. Positive correlation between a focal male's distance to natal nest and distance to father ($F = 295.42$, $P < 0.0001$, $n = 36$)

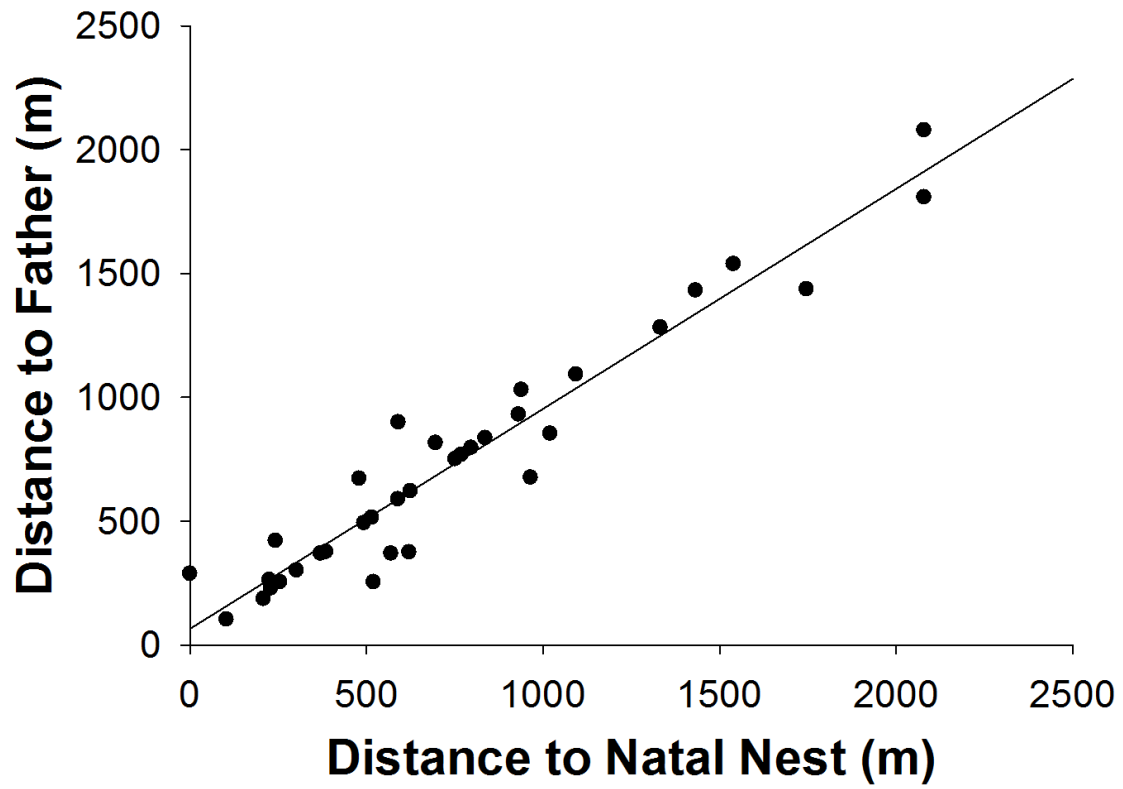


Figure 3. Significant difference between natal dispersal of males with fathers at the natal nest and males with fathers that did not return to the site ($t = -2.50$, $P < 0.02$, $n = 51$). The average distance of each group (father absent and father present) is presented.

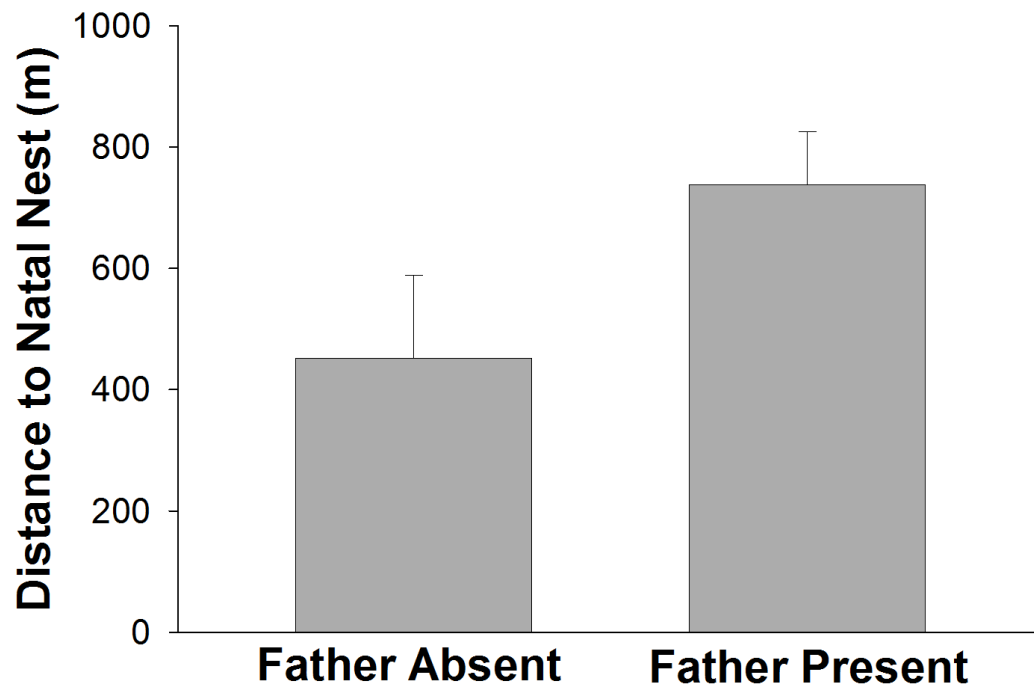


Figure 4. Significant relationship between box density within a 150 m radius around the natal nest and distance dispersed from the natal nest (GLM: $F = 3.76$, $P < 0.03$, $n = 63$)

