Is Territory Switching Adaptive?
Effects of Predation on Within-Season Nesting Dispersal in Barn Swallows,
Hirundo rustica erythrogaster

By
Kyle Donahue
Department of Ecology and Evolutionary Biology,
University of Colorado at Boulder

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Thesis Advisor:
Rebecca Safran, PhD, Department of Ecology and Evolutionary Biology

Defense Committee:
Rebecca Safran, PhD, Department of Ecology and Evolutionary Biology
Barbara Demmig-Adams, PhD, Department of Ecology and Evolutionary Biology
Sona Dimidjian, PhD, Department of Psychology and Neuroscience
Iris Levin, PhD, Department of Ecology and Evolutionary Biology

Abstract

Many animals are territorial during the breeding season. The defense of a particular territory is often dynamic, leading to a pattern of territory switching during, or between, successive breeding attempts. Territory establishment and defense are viewed as costly behaviors, and questions remain about the potential factors leading to, as well as the benefits of, territory switching. One factor influencing such movement is the avoidance of predation. Avian species with multiple clutches provide a good system to study how predation influences territorial movements within a breeding season. I observed a color-banded population of barn swallows (*Hirundo rustica erythrogaster*) in Boulder County, Colorado and quantified predation events, the number of fledglings from each nest, and the distance between the first and second nests. I was specifically interested in how predation influences within-season movement in the barn swallow. I found that predation does not influence the frequency of moves to different nests for a second clutch. However, I did find that as the distance between the first and second nest increased, reproductive success of the second clutch decreased. I also found that predation does not influence whether birds move within or outside of their estimated territories. Finally, I found no difference in reproductive success depending on the decision to move or to stay for a second clutch. These results suggest that predation has little to no effect on barn swallow decisions to move to a different nest for a second clutch. Thus, pairs may be able to assess high-risk predation zones and select nest sites accordingly, reducing their need to disperse to more distant nests for a second clutch. Other factors, such as the ubiquity of the northern fowl mite (*Ornithonyssus sylviarum,* a common nest parasite), and individual variation in territory size, may give further insight

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into the inherently widespread trend of movement between nests in Colorado barn swallows.

Glossary of terms

Breeding-site fidelity: The propensity of adults to return to their previous breeding-site location after the first breeding season.

Clutch: Number of eggs in a nest.

Depredate: A predation event (same as "destroyed by predators") in which eggs or nestlings are killed or eaten in the nest.

Dispersal: Movement of an individual (within or between breeding seasons) from one breeding location to another.

Divorce: Dissolution of socially paired breeding birds that are normally monogamous for one or more breeding seasons.

Fledgling: Young bird that has recently left the nest and is still reliant on its parents to some extent, and has distinct differences in feather color compared to adults.

Nearest neighbor distance: Measurement from a focal nest to the closest active nest.

Nestling: Young bird still in the nest that is unable to feed itself and is completely reliant on the parents.

Parasite: In this study, mites of the genus *Ornithonyssus* that live on the blood of adult birds and nestlings that can lead to a reduction in fitness (Møller 1990a). Also called an *ectoparasite* because they live on the outside of the host organism.

Reproductive Success: A measure of reproductive performance based on the number of offspring produced. In this study, reproductive success is measured as the number of nestlings in the nest on the twelfth day in the nest (just before fledging).

Territory: "an area…over which [an individual] has exclusive or priority use" (Whitaker

and Warkentin 2010).

Introduction

      For many different species of animals, territorial behavior is an important component of life history that can increase survival and reproductive success (see glossary) (Nice 1941, Noble 1939, Bowler and Benton 2005). A territory can be defined as "an area…over which [an individual] has exclusive or priority use" (Whitaker and Warkentin 2010). There is much variation in the size and type of resources that are contained within a territory (Myers *et al.* 1979), such as a small, encompassed area around a nest (e.g., night-herons, Nycticoracinae; Sibley 2001, Nice 1941), feeding locations (e.g., black-backed jackals, *Canis mesomelas*; Nel *et al.* 2013), areas suitable for sexual displays (e.g., superb bird-of-paradise, *Lophorina superba*; Diamond 1986), and even mates themselves (e.g., cardueline finches, Carduelinae; Sibley 2001). An organism may choose to select a nest site within its own territory, a new territory, or one from a nearby, or far-away territory of a conspecific (Nice 1941, Whitaker and Warkentin 2010).

      There are many costs and benefits associated with territorial behavior (Nice 1941, Myers *et al.* 1979, Davis and Brown 1999, Bowler and Benton 2005). An important benefit is having control of nearby resources for the territory holder, as well as any associated mates and offspring (Nice 1941). On the other hand, maintaining a territory is energetically expensive, especially in social or colonial populations, where contact between individuals is frequent and competition may be costly (Myers *et al.* 1979, Davis and Brown 1999). Therefore, an individual must balance the costs and benefits of territorial behavior in order to maximize reproductive success during the breeding season (Bowler and Benton 2005).

In breeding populations with multiple reproductive opportunities over the course of one breeding season, individuals may either remain in the same territory for successive breeding attempts, or move to a different territory. Movement between reproductive attempts can occur between seasons (e.g., goldeneyes, *Bucephela clangula*; Dow and Fredga 1983), or within a single breeding season (e.g., stonechats, *Saxicola torquata*; Greig-Smith 1982, and Indian wolves, *Canis lupus pallipes*; Habib and Kumar 2007). Multiple reproductive attempts per season may also increase seasonal reproductive performance for many species (e.g., barn swallows, *Hirundo rustica*; Shields 1984, wrentits, *Chamaea fasciata*; Guepel and DeSante 1990, hooded warblers, *Wilsonia citrine*; Howlett and Stutchbury 1997, black-throated blue warblers, *Dendroica caerulescens*; Nagy and Holmes 2005, and Louisiana waterthrush, *Seiurus motacilla*; Mulvihill *et al.* 2009). Therefore, organisms that utilize the reproductive strategies of nest switching (either between or within territories) and multiple clutches (see glossary) may increase reproductive success during a single breeding season. However, these two important intra-season reproductive strategies are rarely studied together (Eggers *et al.* 2006, Peluc *et al.* 2008, Lima 2009, Chalfoun and Martin 2010). Questions remain about why animals switch territories and whether this strategy is beneficial in terms of seasonal reproductive performance.

The reasons individuals switch to new territories may include gaining access to new food sources (e.g., army ants, *Eciton burchelli*; Franks and Fletcher 1983), reducing competition (e.g., brown anole, *Anolis sagrei*; Calsbeek 2009), avoiding disturbances (e.g., Habib and Kumar 2007), reducing ectoparasite (see glossary) infestation (e.g., soprano pipistrelle, *Pipistrellus pygmaeus*; Bartonicka 2007), and escaping predation

(e.g., Eastern cottontail, *Sylvilagus floridanus*; Bertolino 2011, pinyon jays, *Gymnorhinus cyanocephalus*; Marzluff 1988, and various other avian species, Greig-Smith 1982, Dow and Fredga 1983, Lima 2009, Hua *et al.* 2013). These switching strategies could be adaptive if the fitness benefits of moving outweigh the costs of staying at the same breeding site (Bowler and Benton 2005). Of the possible reasons to switch breeding sites, predation risk is commonly observed as an important factor predicting territory switching within a breeding season (Lima 2009). One strategy to avoid predation is to move to a more concealed nesting site (Marzluff 1988, Howlett and Stutchbury 1997, Tarvin and Garvin 2002). Another territory switching strategy may involve moving to a new nesting site farther away from the one that was previously destroyed by predators (Greig-Smith 1982, Dow and Fredga 1983, Howlett and Stutchbury 1997).

Equally important in predicting within-season territory switching is the spatial context of the breeding site, as available nest sites may be limited. For instance, some birds breed in large, open habitats that allow for pairs to move far away from a predation event (Greig-Smith 1982, Dow and Fredga 1983, Howlett and Stutchbury 1997, Chalfoun and Martin 2010). Others are spatially constrained, such as is the case for the barn swallow (*Hirundo rustica*), with nests restricted to particular locations within human-built structures, including buildings and culverts (Shields 1984, Brown and Brown 1999, Safran 2004, Safran 2007). Breeding-site fidelity (see glossary) can also play an important role in spatial restrictions and reproductive success. For instance, barn swallows very rarely change breeding sites after their first breeding season, further limiting the ability to disperse (see glossary) to novel nesting sites (Darley *et al.* 1971, Shields 1984, Brown and Brown 1999, Safran 2004). Much is unknown about these

restricted dispersal systems, but it is possible that these limitations may increase the importance of the decision to switch nests within a season for barn swallows in order to maximize reproductive success (Shields 1984, Eggers *et al.* 2006, Lima 2009, Chalfoun and Martin 2010).

Barn swallows return each year to the location (barn, bridge, building) of their first breeding attempt despite the removal of nests, important resources related to territory quality (Shields 1984, Safran 2004, 2006, 2007). Barn swallows construct open cup nests comprised of hundreds of mud pellets interwoven with hay and horse hair that can persist in the environment for many years and are often reused by the same or different breeding pair over the course of a decade or more (Shields 1984, personal observation). The presence and quantity of old nests attract females in their first breeding year (Safran 2007). Not surprisingly, pairs prefer existing nests, which may minimize energy expenditure on the construction of new nests (Safran 2006, Ringhofer and Hasegawa 2013). However, in an effort to avoid nests with overwintering parasites (*Ornithonyssus* spp.) or because they cannot successfully compete for access to an existing nest, some pairs will construct new nests throughout the breeding season despite the associated energy costs (Møller 1990a, Safran 2006 and unpubl. data,).

In the present study, I examine barn swallows (*Hirundo rustica erythrogaster*) at three different breeding locations in Boulder County, Colorado. Barn swallows are small (17 to 20 g), migratory, insectivorous passerines with a high degree of breeding-site fidelity, making them tractable for behavioral study (Brown and Brown 1999, Safran 2004). They breed in open cup-nests built on barn walls and rafters, under bridges, and on the sides of homes, which makes it easy to monitor clutch size and reproductive success

(measured as the number of fledglings, see glossary). This New World subspecies of barn swallow begins migrating to North America in mid-February, after wintering in Central and South America. Males are typically the first to arrive on the breeding grounds to claim and defend territories, allowing them to mate with the later-arriving females (Brown and Brown 1999, Safran 2007). Both sexes aid in nest preparation, which includes selecting white feathers to line the nest and incubation (Brown and Brown 1999). Pairs can go on to have a second clutch, and in some cases, up to four clutches in one breeding season (Shields 1984, Brown and Brown 1999). Within-season divorce (see glossary) is rare (Shields 1984, personal observation). Breeding colonies can range anywhere from 2 to 200 pairs (Cramp 1988, Safran 2004). Individuals depart for the wintering grounds between August and October (Brown and Brown 1999).

Barn swallows are exposed to various types of predation. These include predators introduced to the Americas, such as domestic cats, house sparrows (*Passer domesticus*) that repossess swallow nests and evict the contents, and European starlings (*Sternus vulgaris*) that peck eggs and new fledglings to death. Other predators include snakes (e.g., gopher snakes, *Pituophis catenifer*), raptors (e.g., red-tailed hawks, *Buteo jamaicensis*, and European sparrowhawks, *Accipiter nisu*), and corvids (e.g., black-billed magpies, *Pica hudsonia*) (Møller 1987, Brown and Brown 1999, personal observation).

My study focuses on the adaptive significance of territory switching within a breeding season with respect to predation. First, I hypothesized that predation influences nest switching between clutches, and that birds are more likely to move if predators destroyed their first clutch. Second, I hypothesized that the distance between the first and second nests is a result of the reproductive performance of the first clutch. Furthermore,

the distance moved also affects reproductive performance of the second nest. As the distance between the first and second nest increases, then so should reproductive performance if predators destroyed the first clutch. Third, I hypothesized that predation would influence a pair to move outside of their territory for a second clutch (as opposed to staying and renesting, or moving within the territory). Last, I hypothesized that nest movement between clutches influences reproductive performance. Birds that move after predation of their first clutch will have higher reproductive performance in a different nest compared to birds that remain in their original nest for a second clutch. My questions, hypotheses, and predictions are summarized in Table 1.

Materials & Methods

Field methods

I examined barn swallows in Boulder County, Colorado, U.S.A, from early May through late August in 2014. I also used a long-term data set from 2008 to 2013. Barn swallows were captured by mist-netting and night captures of sleeping birds on the nest. Birds were then banded with USFWS metal bands and multicolored Perler® beads in order to individually identify birds in the field. I also marked the white tail spots with a colored nontoxic marker (Sharpie®) in order to identify breeding pairs and the nests they were defending. I minimized the birds' time in hand to reduce overall impacts of stress.

Each nest was checked twice a week to quantify the number of eggs or nestlings (see glossary). This was done with a mirror attached to a long, extendable pole. I estimated hatching dates as two weeks from when the penultimate egg was laid. From the estimated hatch date onward, I checked the nest every day to best estimate the actual hatch date. I was careful not to flush nestlings from the nest later in their development.

For every active nest, I made observations of the identity of the pair that was utilizing the nest. I monitored nests up until a few days before fledging to prevent nestlings from prematurely leaving their nest. Once nestlings fledged, I rechecked the nest to determine whether it was empty or whether unhatched eggs or dead nestlings remained. This was repeated for every active nest throughout the course of the season. Nestlings were banded with USFWS bands on the twelfth day after hatching. Throughout, the number of nestlings in the nest on the twelfth day indicates an individual's reproductive success.

Predation and egg collection

I inferred a predation event when nestlings or eggs disappeared from the nest. Predation was the only plausible form of offspring loss if no eggs or nestlings were found on the ground underneath the nest, which typically happens when a smaller nestling is ejected by its nest mates or parent, or fails to fledge successfully. Eggs were collected from nests at two sites during the season of 2009 in order to synchronize female laying dates. I included the data from these collection experiments with predation data and checked that this type of human-induced "predation" did not differ from naturally occurring nest predation (e.g., Safran *et al.* 2005).

Site measurements

In order to measure distances between nests at such high densities in difficult to reach locations, I measured the layout of the barn with a Bosch® DLR130K Laser Distance Measurer and created digital maps using the program SketchUp Make, v.15.3.329 (Trimble Navigation Limited 2015). I also measured each nest from its base at the supporting structure to the nearest landmark inside the barn in order to position them accurately on the digital map. Once the map was finished, I used the tape measuring

function of SketchUp to measure the pair-wise distances between all nests. Nearest neighbor distances (see glossary) were also measured using the tape measuring function. Only the first clutch nests, and not the second clutch nests, were used to determine the nearest neighbor distances as males claim their territory around the first nest, and later move to a second nest; these events are temporally separated and first nesting attempts tend to be synchronous (Brown and Brown 1999).

Estimating territory size

In order to determine whether or not pairs were moving outside of their estimated territory during nest switching, I calculated all nearest neighbor distances for each site within each year. I then used the median of the nearest neighbor distances for each site as a site-specific estimated threshold distance for determining barn swallow territory size, as the size of the barns and density of nests vary by site. Distances between first and second nests that were greater than the site-specific threshold were considered out-of-territory moves, while those that were less than the threshold were classified as within-territory moves. The median was used in order to account for the very distant and the very close neighbor nests in order to obtain a more conservative estimate of territory size. Histograms of site-specific nearest neighbor distances can be found in the appendix (Figures A1 – A3). Additionally, Figure A4 compares nearest neighbor distances among the three sites.

Statistical analysis

All data were analyzed in R v.3.1.2 (R Development Core Team 2014). I used contingency tables and chi-square tests to test for differences in the count data for nest switching, such as "move" or "stay" decisions for a second clutch. Generalized Linear Models and Linear Models were used in the instances of between-nest movement to see if the distance between first and second nests, as well as with categorical data (nests destroyed by predators are indicated by a '0' and nests with fledged young are indicated by a '1'), correlated with reproductive success. Additionally, I used independent Student's t-tests to measure the differences between mean reproductive success of birds that moved to a new nest for their second clutch, and those that decided to stay in the first nest for a second clutch.

Results

Hypothesis 1: Predation and its effects on the decision to move

Overall movement

There were no statistical differences among the three breeding sites in the number of movements from the first nest to the second nest in cases where there was a second clutch, regardless of the fate of the first clutch (Table 2, chi-square test: $\chi^2 = 0.02$, df $= 1$ p-value $= 0.89$). This allows for the nest movement data from three separate sites to be combined into one data set for analysis of movement patterns with a larger sample size. The median distances moved between nests are shown for each site in Figure 1. Histograms of the distances moved between nests for each site are found in the appendix (Figures A5 – A7).

Predation and decision to move

Predation did not influence the pairs' decisions to move to a different nest for a second clutch (Table 3, chi-square test: $\chi^2 = 0.09$, df $= 1$, p-value $= 0.76$, n $= 204$). In this case, I did not consider within vs. outside-of-territory moves.

Hypothesis 2: Distance moved and its effects on reproductive success

Reproductive success of first clutch and distance moved

There was a weak, negative association between the success of the first nest and the sequential distance moved to the second nest, indicating that a pair's poor reproductive success in the first nest was associated with a greater distance moved to the second nest (Linear Model: Adjusted $R^2 = 0.029$, F $= 4.90$, df $= 130$, p-value $= 0.03$, n $= 131$). However, when I removed an unusually large distance moved between nests, 25 meters, this trend disappeared (Linear Model: Adjusted $R^2 = 0.004$, F $= 1.46$, df $= 129$, p-value $= 0.23$, n $= 130$).

Distance moved and reproductive success of second clutch

There was a weak, negative association between the distance moved between the first and second nests and the number of fledglings of the second clutch, indicating that birds that moved farther from their first nest had a decrease in reproductive success in the second nest (Figure 2, Generalized Linear Model: Null deviance: 168.84, df $= 124$, residual deviance 161.37, df $= 123$, z-value $= -2.447$, AIC $= 494.08$, p-value $= 0.01$, n $= 123$).

Hypothesis 3: Predation and territory switching

Fate of first nest and decision for second clutch

Predation did not influence the pairs' decisions to stay in the same nest or make a territorial vs. non-territorial switch. (Table 4, chi-square test: χ^2: 0.04, df = 1, p-value = 0.84). Thus, the outcome of the first nest (destroyed by predators or successfully fledged) had no effect on the decision to move to a different nest, whether it was outside or inside the pairs' territory, or the decision to stay in the same nest for a second clutch.

Hypothesis 4: Decision to move and reproductive success of second clutch

There was no significant difference between the decision to move or stay and the mean number of chicks fledged after the first nest was depredated (see glossary), even though the mean number of fledglings was greater for birds that moved nests than for the birds that stayed in the same nest for another clutch (3.53 and 2.52 respectively) (Figure 3, independent Student's t-test: t = 1.78, df = 46, p-value = 0.08). Furthermore, there was no significant difference between the mean numbers of chicks for all birds that moved nests, regardless of predation of first clutch, and for the birds that stayed in the same nest for another clutch (3.07 and 2.86 respectively) (Figure 4, independent Student's t-test: t = 0.91, df = 221, p-value = 0.37).

Discussion

I found that, regardless of the fate of the first clutch, there were no statistical differences among the three breeding sites in the number of movements from the first nest to the second nest, in cases where there was a second clutch. Further, I found that predation did not influence the pairs' decisions to move to a different nest for a second

clutch. However, I found that the success of the first nest and the subsequent distance moved to the second nest showed a weak, negative relationship, but this was not significant when a move of 25 meters was removed from the analysis. I also found a slight reduction in reproductive performance of birds that moved farther from their first nest, which was still significant when the outlier of 25 meters was removed. When considering territory size, I found that the outcome of the first nest, whether it had been destroyed by predators or fledged successfully, had no effect on the pairs' decisions to stay at the original nest or move — within or outside the territory — to another nest. Finally, I found no differences in mean reproductive success when looking at the birds' decisions to move after the first nest was destroyed by predators or fledged successfully. The three breeding sites I examined had the same high rates of movement between nests, indicating that in the instance of a second clutch, moving to a different nest is more common than renesting in the same nest. Furthermore, this rate of within-season movement is high compared to another well-studied population of barn swallows in Ithaca, NY, where pairs rarely switch nests outside of their original territory during the breeding season (Safran, unpubl. data).

Hypothesis 1: Predation and its effects on the decision to move

I did not find support for the hypothesis that predation in the first breeding attempt induces movement to a different nest site. Fisher and Wiebe (2006a) reported very similar results; Northern flicker pairs do not move nesting cavities within-season following a nest predation event. There were striking similarities between Fisher and Wiebe's (2006a,b) studies and the present study, both in terms of the rate of predation (18% in theirs and 17% in this study) and the primary predator itself, the European

starling (Fisher and Wiebe 2006b). There are several explanations for why pairs are equally likely to switch nests regardless of whether predators destroyed their first clutch. One explanation is that the birds are already successful at avoiding predation when they select their nest site, such as Siberian jays' (*Perisoreus infaustus*) ability to settle in a nest with more protection in response to call-back experiments of nest predators (Eggers *et al.* 2006). The number and location of the starlings, due to their conspicuous calls and presence, might provide important cues about predation risk to barn swallows when they are selecting a nest site. There could be "hot spots" of predation, such as near the nests of starlings, where nearby swallow nests may be at a higher risk of predation than those farther away. During field observations, I witnessed several adult starlings attack newly fledged barn swallow chicks trespassing on their territories. Therefore, barn swallows may already be avoiding these "hot spots" and any observed nest switching is unrelated to avoiding predation.

Alternatively, dynamic patterns of predation might explain within-season nest switching. Nest switching might allow pairs to avoid detection by not staying in a place for too long (e.g., Sonerud 1985). The observation of high levels of movement in nests that were not destroyed by predators may suggest that movement is an inherent predator avoidance strategy in the focal barn swallow population. Predation avoidance could therefore be driven not by a response to actual predation events, but rather by the anticipation of predation.

Other studies have shown that pairs can respond to depredation of their first clutch by nest switching. In a study by Dow and Fredga (1983), female goldeneyes were twice as likely to nest in a different nest when their previous nest was depredated the year

before. Even though this effect is between years, it indicates that females can respond to the outcome of the first nest and choose a different nest for a new clutch. Moreover, pinyon jays were found to change nesting location, height, and nest-opening concealment depending on the specific predator encountered (i.e., domestic cats vs. other corvids; Marzluff 1988). Whatever the specific nesting response may be, a common pattern in many avian species is movement to a different nest within the same breeding season following failure of the first nest due to predation or other factors (Marzluff 1988, Forero *et al.* 1999, Stanback and Dervan 2001, Lima 2009).

Contrary to my findings, Shields (1984) found that barn swallows that had a successful first clutch were more likely to move to a different nest. The reason for this may be the prevalence of northern fowl mites, common nest parasites that feed on nestlings. These nest mite populations undergo rapid growth during the barn swallow breeding season. Mite abundance peaks just before nestlings fledge, acting as a deterrent for renesting in the same nest (Shields 1984, Møller 1990a, Safran 2006). Møller (1990a) further suggests that barn swallows occupying nests more heavily infested with mites switch nests more often. However, there is evidence of mites hitchhiking on adults and reinfesting subsequent nests, indicating an inability to escape the ubiquitous parasites. Whether or not barn swallow pairs are moving as a consequence of predation or parasites, or perhaps a function of both, warrants further investigation.

Hypothesis 2: Distance moved and its effects on reproductive success

Success of first clutch and the distance moved

My results showed that there was a weak, negative association between the fate of nest one and the distance moved to nest two; pairs with successful first clutches moved

shorter distances to a different nest than pairs whose first breeding attempts failed. However, when I removed an unusually great distance between the first nest and the second nest (25 meters) from the data set, the trend disappeared. Perhaps the high frequency of movement between nests obscures any effect of predation of the first nest.

Contrary to my findings, other studies on the effects of predation on nest switching in a number of different bird species find that predation of the first nest induces movement to a new location, often far from the site of the depredated nest. For example, when predators destroyed their first clutch, stonechats were found to disperse to farther nests (Grieg-Smith 1982), and great tits were more likely to move out of their territory after their first nest was destroyed by predators (Harvey *et al.* 1979). Grey catbirds also followed this trend when their first clutch failed, but the causes of clutch failure were grouped together so the full effects of predation were lost (Darley *et al.* 1971). It could be easier for birds with large expanses of territory to escape a predation event. However, this is unlikely in barn swallows, as nesting sites are constrained by the structures that individuals reside in. Predators may easily track within-season movements of barn swallows, potentially negating any relationship between the distance of the move and reproductive success (personal observation).

Distance moved and reproductive success of second clutch

Pairs that moved farther between first and second nests for a second clutch had reduced reproductive success compared to pairs that stayed closer to their first nest location. This is contrary to what I originally expected; I had predicted that, by moving farther away from predators, individuals would increase the likelihood of nestling survivorship and decrease the likelihood of another predation event. There are several

hypotheses that explain this unexpected finding. One potential reason why reproductive success might decline with increased distance from a pair's original nest is that moving within an area might increase the risk of detection by predators through increased activity (Bowler and Benton 2005). However, this is unlikely in barn swallows due to their already overt sociality and movement. Additionally, stonechats that dispersed farther after a predation event in the first nest had higher chances of second clutch failure, attributed to the increased chance of nesting near predators (Grieg-Smith 1982). Unlike stonechats, the Colorado barn swallow populations in this study have small territories that are restricted to areas immediately surrounding the nest, all encompassed by structures that are also typically occupied by many other pairs. Therefore, dispersal away from predators might be constrained by the physical space and small territory sizes of the males.

Second, barn swallows are territorial (Shields 1984, Møller 1990b); males establish their territories relative to other males early in the season. There may be costs associated with moving away from a successfully established territory with familiar birds to a different nest in a new territory, in which the male must again fight for control. This male-to-male interaction may lead to a decrease in second clutch reproductive success (Shields 1984) if, for example, it diverts energy away from caring for the chicks. This type of territorial behavior has been described by the "Dear Enemy" Hypothesis (Fisher 1954). Interestingly, in a review of the "Dear Enemy" Hypothesis, Temeles (1994) found no evidence for the hypothesis within the densest colonies of nesting seabirds. However, at greater nearest neighbor distances, Temeles (1994) did find support for the "Dear Enemy" Hypothesis for a variety of colonially nesting seabird species that tend to be less

spatially clustered. The mean nearest neighbor distances that I calculated for the barn swallows fall right between the distance categories that either show support for, or against, the "Dear Enemy" Hypothesis reported by Temeles (1994). If there is some distance threshold that influences interactions with neighbors, it is difficult to predict whether barn swallows ought to tolerate their neighbors based on the evidence presented in Temeles (1994).

There are also potential costs associated with moving farther away from the familiarity of the first nest. Consistent with the "Dear Enemy" phenomenon, an individual could expect their neighbors to respect their territorial boundaries, therefore reducing energy spent in defense (Fisher 1954, Shields 1984, Temeles 1994). Familiarity with the local environment may also increase reproductive success; spotted antbirds (*Hylophylax naeviodes*) that nest in previously successful nests avoid recently depredated nests (Styrsky 2005, Lima 2009). Barn swallows that remain near their original nest may benefit socially by avoiding conflict with their neighbors as the season progresses, or by being better able to assess predation risk due to site familiarity. More research is needed to understand male-to-male territorial behavior and the effects of neighbor familiarity to determine whether a "Dear Enemy" effect is a contributing factor in decreasing the reproductive success of the second clutch of barn swallows.

Hypothesis 3: Predation and territory switching

I found that the outcome of the first nest, whether it had been destroyed by predators or fledged successfully, had no effect on the pairs' decision to stay at the original nest, or move to a new nest, regardless of the type of move (within vs. outside the territory). Considering that predation has no effect on decisions to move to another

nest for a second clutch, the result that predation does not influence territory switching is not very surprising. However, I did find a very weak relationship between the distance moved between nests and reproductive performance of the second nest. An interpretation of this trend is that pairs should remain within their territory in order to maximize reproductive success. Therefore, when considering the type of move (within vs. out-of-territory), one should expect fewer out-of-territory moves. However, I found nearly equivalent numbers of within vs. out-of-territory moves. One explanation is that my estimate of territory size is standardized across all pairs and thus does not account for individual differences in behavior or phenotype among males, which has been shown to predict territory quality (more intact and older nests) in North American and Asian populations of barn swallows (Brown and Brown 1999, Safran 2004, Hasegawa *et al.* 2014). In order to accurately characterize territory sizes, male territories need to be assessed in an individual-based manner. Additionally, barn swallow territory sizes seem to be dynamic throughout the breeding season, as territory sizes are smallest when the female is incubating, and largest when she is most fertile (Møller 1990b). Finally, it is possible that territories shift spatially to always surround the current active nest, rather than staying statically fixed around the original nest as reflected in my estimations of territory size. The threshold distances I established, while conservative and site-specific, probably oversimplify the complexity of male territory qualities and dynamics.

A reason to move outside one's territory may be due to within-season divorce. A divorce, although rare in barn swallows, occurs when the social pair-bond is broken when a female decides to abandon a male due to his poor reproductive qualities and select a new mate within the same breeding season (Shields 1984, Choudhury 1995, Safran

2007). Female birds are more likely than males to move between territories (Greenwood and Harvey 1982). I have anecdotal evidence of a within-season divorce in 2014, when a female abandoned her social mate and moved a large distance across the barn to breed with a different male. In this study, I did not consider the identity of the birds in each pair, and instead I assumed pair-bond continuity throughout the season, a reasonable assumption given how rare divorce is in this system. In systems with more frequent divorce, social pair-bonds should be tracked relative to nest switching, reproductive performance, and predation.

Hypothesis 4: Decision to move and reproductive success of second clutch

I found no differences in mean reproductive success when looking at the birds' decisions to move after the first nest was either destroyed by predators or successfully fledged. This finding is consistent with the results from my previous questions; after predation, birds seem to do equally well in the original nest or a different nest. It is surprising that there seem to be no fitness-related costs associated with switching nests. As stated previously, one cost could be heightened territorial behavior by males in new locations. Another cost could be from the creation of a new nest. Building a new nest is thought to occur when there are a lack of old nests due to occupation by other pairs or an abundance of parasitic mites in available nests. Other studies have shown a decrease in reproductive success when pairs build a new nest due to the costs of finding materials, building, and then lining the nest with fresh, white feathers, all the while delaying reproduction (Shields 1984, Barclay 1988, Safran 2006, Mainwairing and Hartley 2013). Barclay (1988) found that barn swallows reproduced equally well in old vs. new nests, arguing that pairs must be able to weigh the costs and benefits of switching nests while at

the same time assessing the nests' mite populations. On the other hand, Safran (2006) found a decrease in reproductive success in old vs. new nests, but also agrees that the birds' ability to assess mite abundance is a contributing factor as to why there is a modest difference in reproductive success. Further research is needed in order to quantify the effects of mites on within-season nest switching and reproductive output of the barn swallow, as it appears that predation has little to no effect on their reproductive success.

Conclusion

During the breeding season, barn swallow pairs must navigate a variety of ecological challenges to optimize seasonal reproductive performance. Despite the prevalence of nest loss due to predators, predation was found to have little to no effect on the decision to move to a different nest, or the reproductive success of second clutches. Predation was also shown to have no effect on within or out-of-territory movement. The occurrence, type, and frequency of predation might be playing a more complex role in nesting behavior than previously thought. For example, some predators are themselves territorial within the same nesting sites as barn swallows (e.g., house sparrows and starlings), whereas others are less tied to the same breeding locations (e.g., magpies), allowing for interactions among predators that are hard to quantify (e.g., Fisher and Wiebe 2006a). Moreover, future studies should assess territory sizes based on more detail, such as timing during the breeding season and the phenotype of the male in order to better understand the effects of predation on territorial movement and reproductive success. Lastly, the presence and overall effects of parasitic nest mites were not directly analyzed in this study, but may likely be an important factor in explaining patterns of nest movement within breeding sites.

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Tables

Table 1. Hypotheses related to predation and within-season nest switching in North American barn swallows.

Questions	Hypotheses	Predictions	Support?	Analyses
1) Does predation influence nest switching?	Pairs whose first clutches were destroyed by predators are more likely to move to a different nest	Pairs with unsuccessful first breeding attempts move more often than pairs with successful first breeding attempts	No	Chi-square $\chi^2 = 0.09$, df = 1, p-value = 0.76 n = 204 (Table 3)
2) a. Does the reproductive performance of the first clutch affect the distance moved to a different nest for a second clutch?	a. The reproductive success of the first clutch affects the distance moved to the second nest	a. Pairs should move farther to a second nest after poor reproductive performance of the first clutch	a. No	a. Linear Model $R^2 = 0.004$, F = 1.46, df = 1 and 129, p-value = 0.23 n = 131
b. Does the distance moved to a different nest for a second clutch affect the reproductive success of the second clutch?	b. The distance between the first and second nests affects reproductive performance of the second clutch	b. As the distance between nest one and nest two increases, then so should reproductive performance of the second clutch	b. Yes (but opposite of prediction)	b. Generalized Linear Model null deviance = 168.84, df = 124, residual deviance = 161.37, df = 123, z-value = -2.45, AIC = 494.08, p-value = 0.01, n = 123 (Figure 2)
3) Does predation influence pairs to move outside of their territories for a second clutch?	Predation influences territorial movement	Predation of the first clutch will influence pairs to move outside of their original territory for a second clutch	No	Chi-square: χ^2: 0.04, df = 1, p-value = 0.84 (Table 4)
4) Is nest switching adaptive?	Nest movement between clutches influences reproductive performance	Birds that move after predation of their first clutch have higher reproductive performance in a different nest, compared to birds that remain in their original nest for a second clutch	No	Student's independent t-test: t = 1.78 df = 46, p-value = 0.08 n = 48 (Figure 3)

Table 2. Descriptive statistics on movement and predation for the three sites.

Site	Years	Depredated first clutches, regardless of presence of a second clutch (%)	Depredated first clutches & pairs had a second clutch (%)	No. nests with eggs collected	Movement from first to second nest (%)	Median nearest neighbor distance (m)
Colorado Horse Rescue	2010-2014	21.48	26.79	NA	62.65	1.966
Golden Grizzly	2009-2014	12.56	3	17	67.24	1.206
Make Believe	2008-2014	20.55	21.21	8	61.11	2.631
All sites	2008-2014	16.95	13.23	25	64.68	NA

Table 3. Numbers of birds that moved vs. stayed for a second clutch based on the fate of the first clutch.

	Depredated	Fledged	Total
Move: Yes	30	106	136
Move: No	17	51	68
Total	47	157	204

Table 4. Nesting decisions for second clutches based on the fate of the first clutch.

Decision for second clutch	Fate of first nest		Total
	Depredated	Fledged	Total
Stay	17	49	66
Move within territory	16	45	61
Move outside territory	15	58	73
Total	48	152	200

Figures
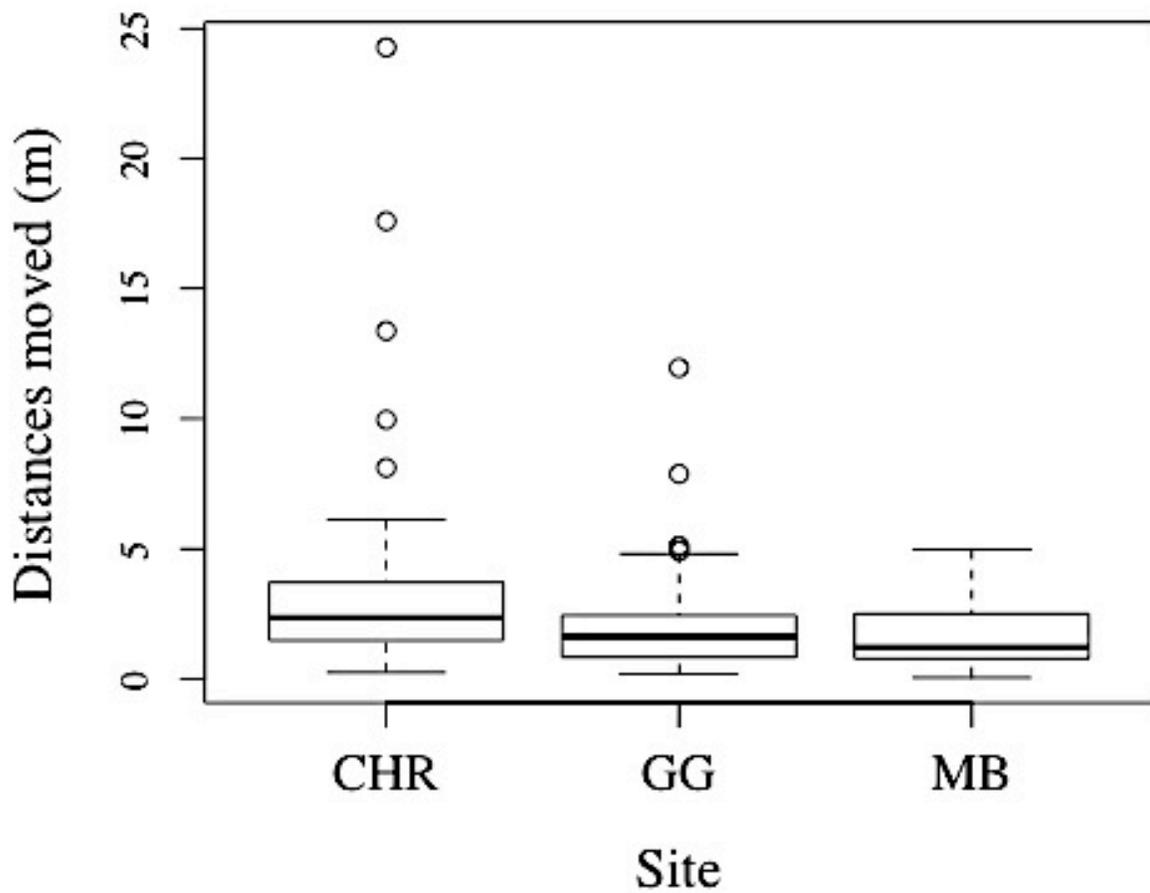
Figure 1. Comparison of the median movement distances between nest one and nest two in meters at each site. Colorado Horse Rescue (CHR), Golden Grizzly (GG), and Make Believe (MB) for the years of 2008 to 2014 (CHR: median = 2.35 m, sd = 4.33 m, n = 51, GG: median = 1.62 m, sd = 1.83 m, n= 74, MB: median = 1.21 m, sd = 1.48 m, n = 22). Boxes show interquartile range, and whiskers show the variability outside of the quartiles. Outliers are represented as individual points.
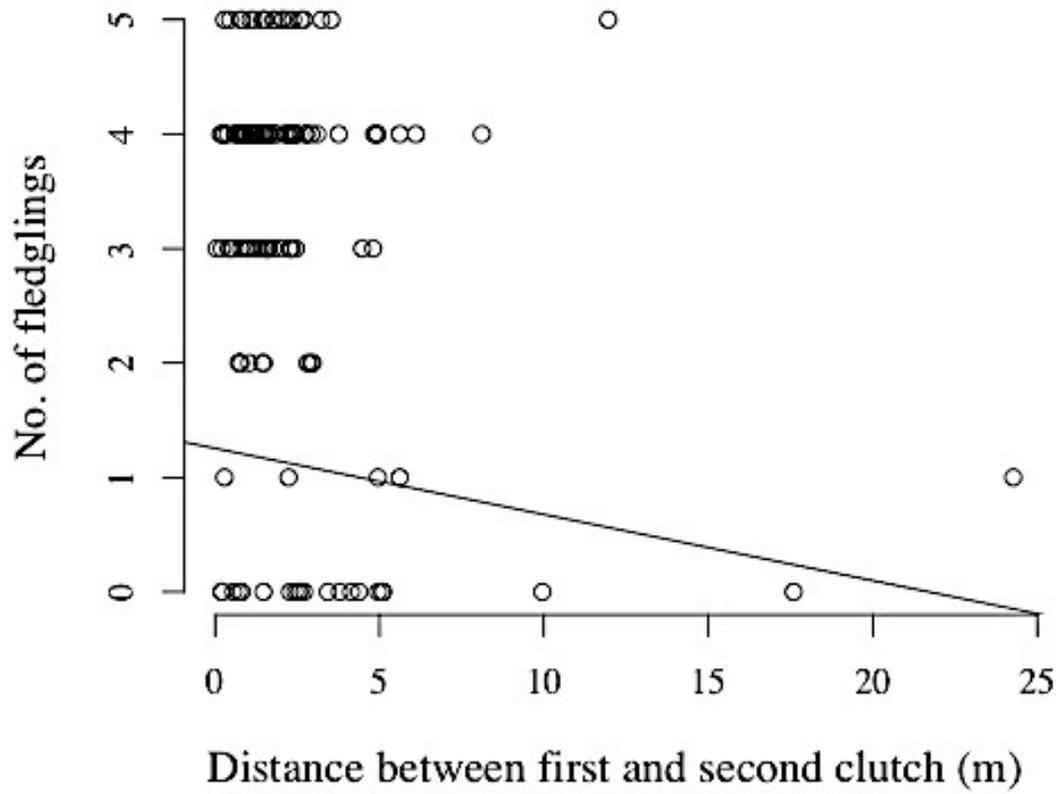
Figure 2. The number of fledglings from the second nest and the distance moved between the first and second nest.
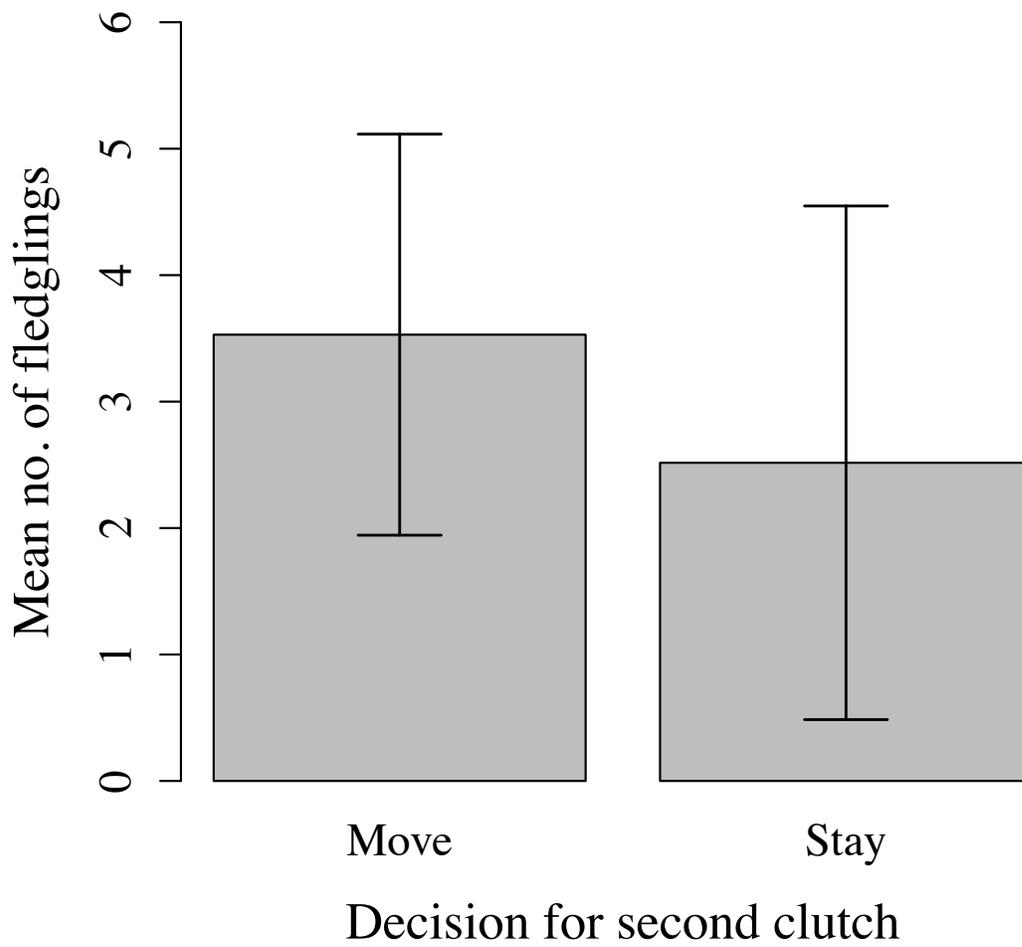
Figure 3. Mean number of fledglings, plus and minus standard deviation, from second clutches as a function of whether pairs moved to a different nest or stayed in the original nest for a second clutch. Data are for first nests that were depredated or collected.
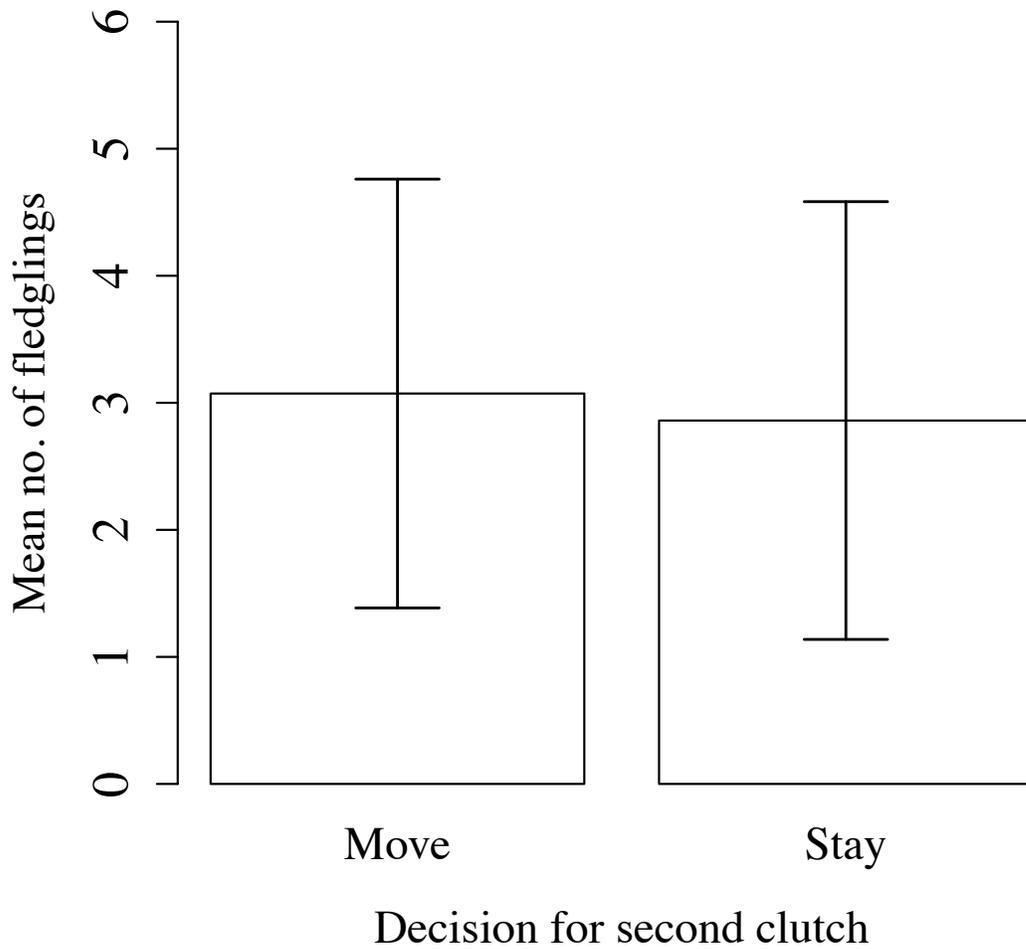
Figure 4. Mean number of fledglings, plus and minus standard deviation, from second clutches as a function of whether pairs moved to a different nest or stayed in the original nest for a second clutch. Data are for all nests, regardless of depredation or collection of first nest.
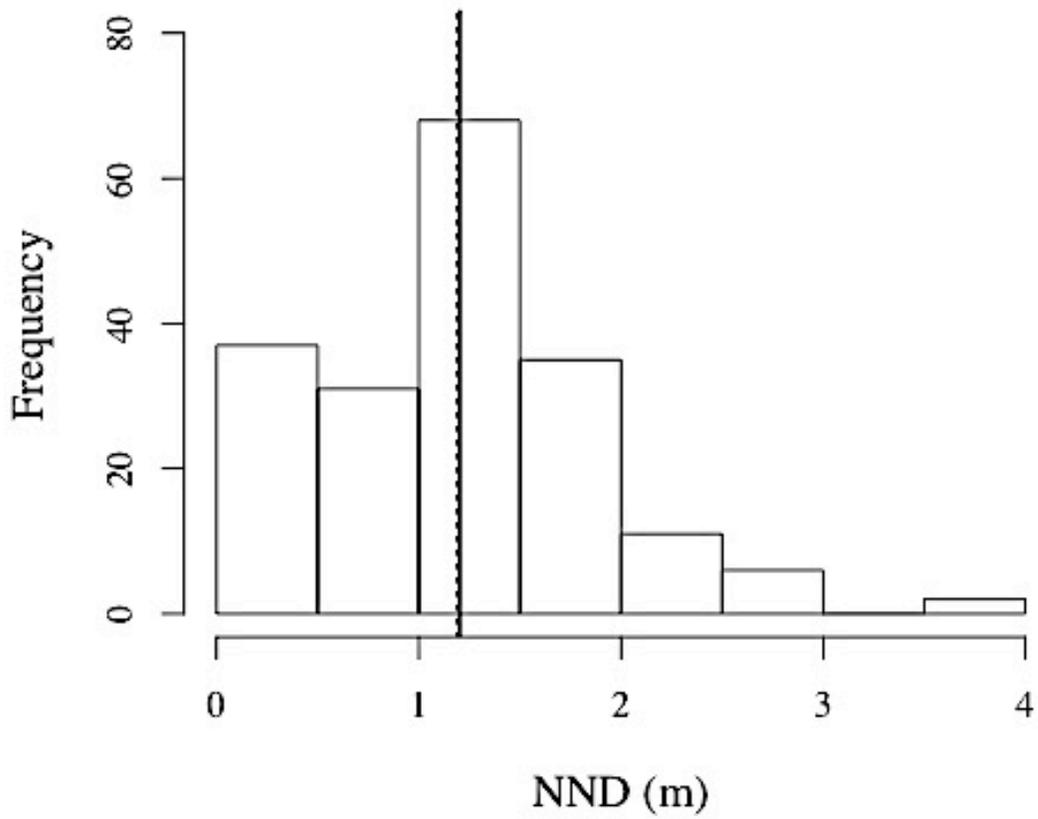
Appendix
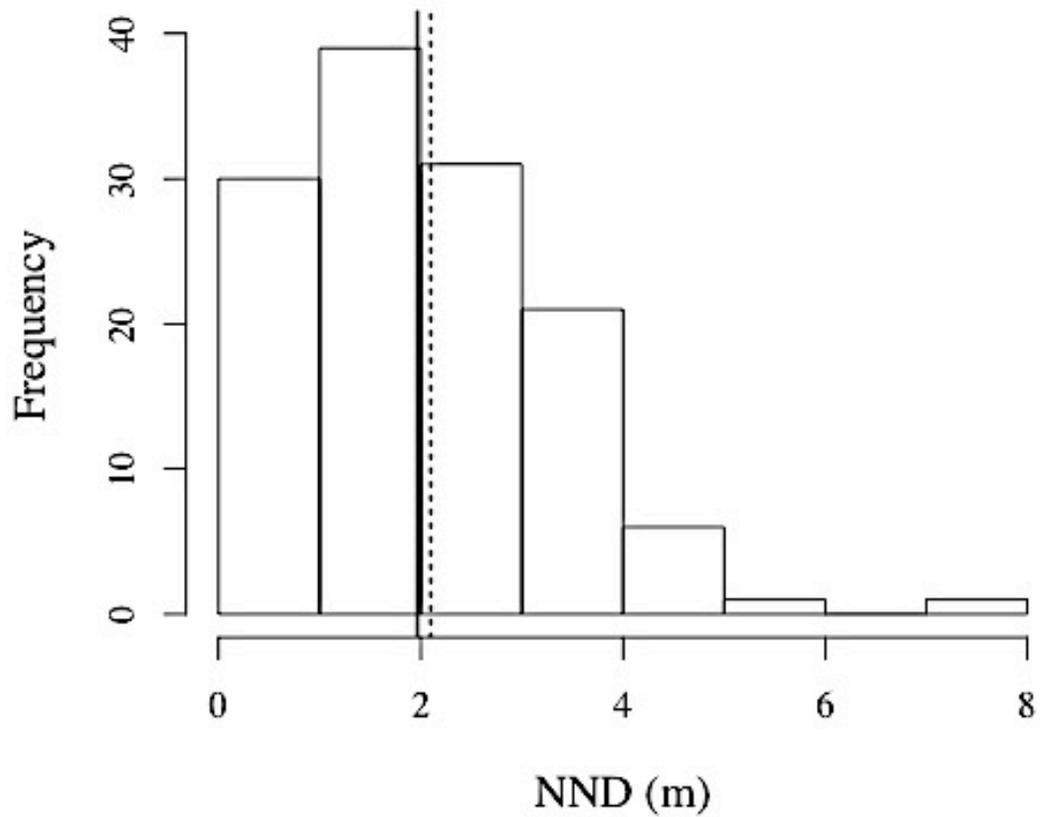
Figure A1. Frequencies of nearest neighbor distances (NND) in meters at one site, Colorado Horse Rescue (CHR), for the years of 2010 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 1.97 m, mean = 2.10 m, sd = 1.26 m, n = 124).

Figure A2. Frequencies of nearest neighbor distances (NND) in meters at one site, Golden Grizzly (GG), for the years of 2009 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 1.20 m, mean = 1.19 m, sd = 1.20 m, n = 190).
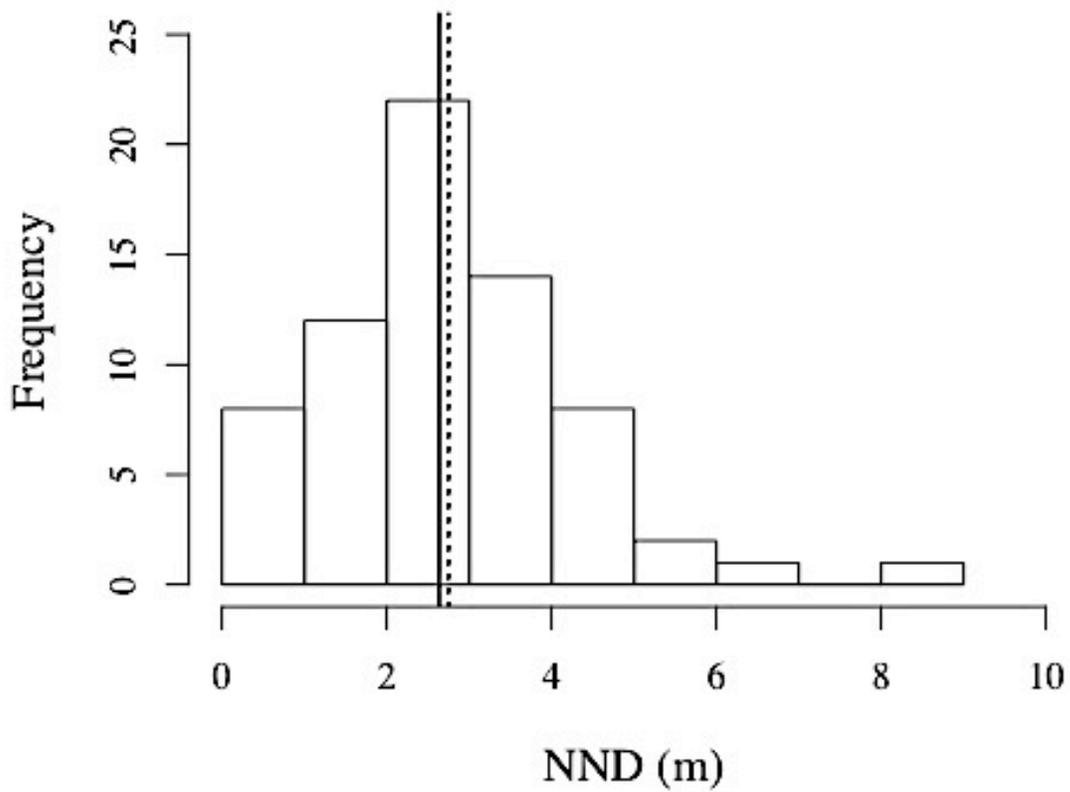
Figure A3. Frequencies of nearest neighbor distances (NND) in meters at one site, Make Believe (MB), for the years of 2008 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 2.63 m, mean = 2.75 m, sd = 1.50 m, n = 68).
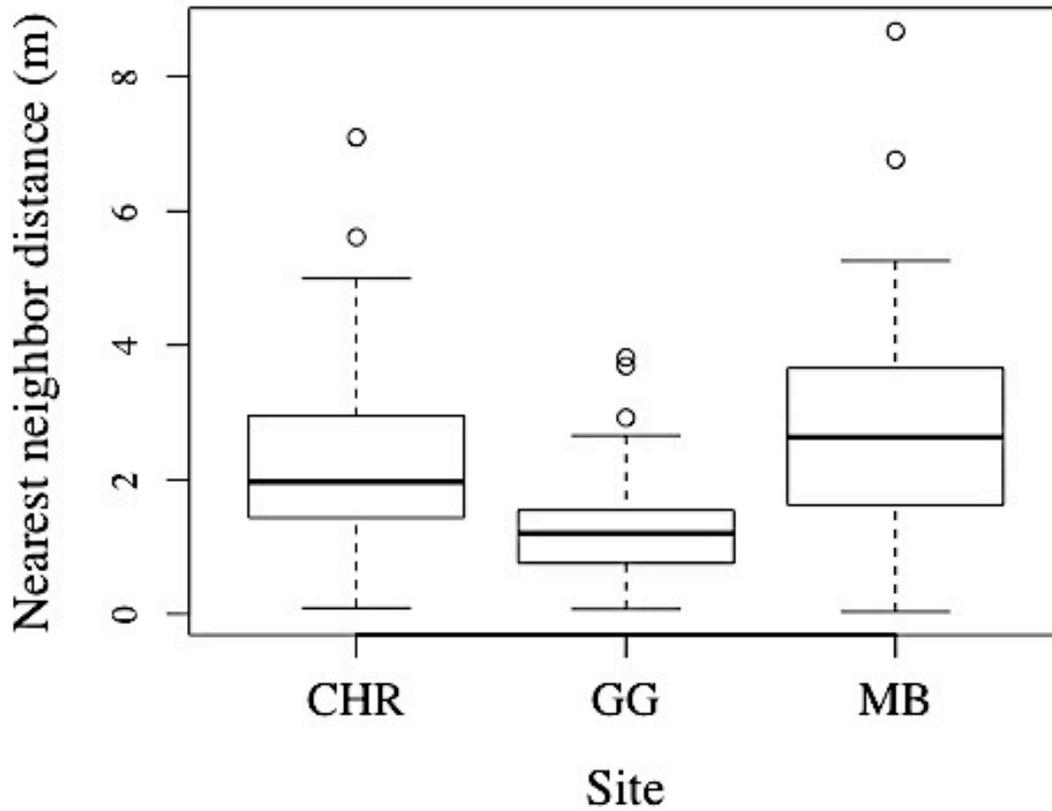
Figure A4. Comparison of the median nearest neighbor distances in meters at each site, Colorado Horse Rescue (CHR), Golden Grizzly (GG), and Make Believe (MB) for the years of 2008 to 2014 (CHR: median = 1.97 m, sd = 1.26 m, n = 129, GG: median = 1.21 m, sd = 0.70 m, n = 190, MB: median = 2.63 m, sd = 1.50 m, n = 68). Boxes show interquartile range, and whiskers show the variability outside of the quartiles. Outliers are represented as individual points.
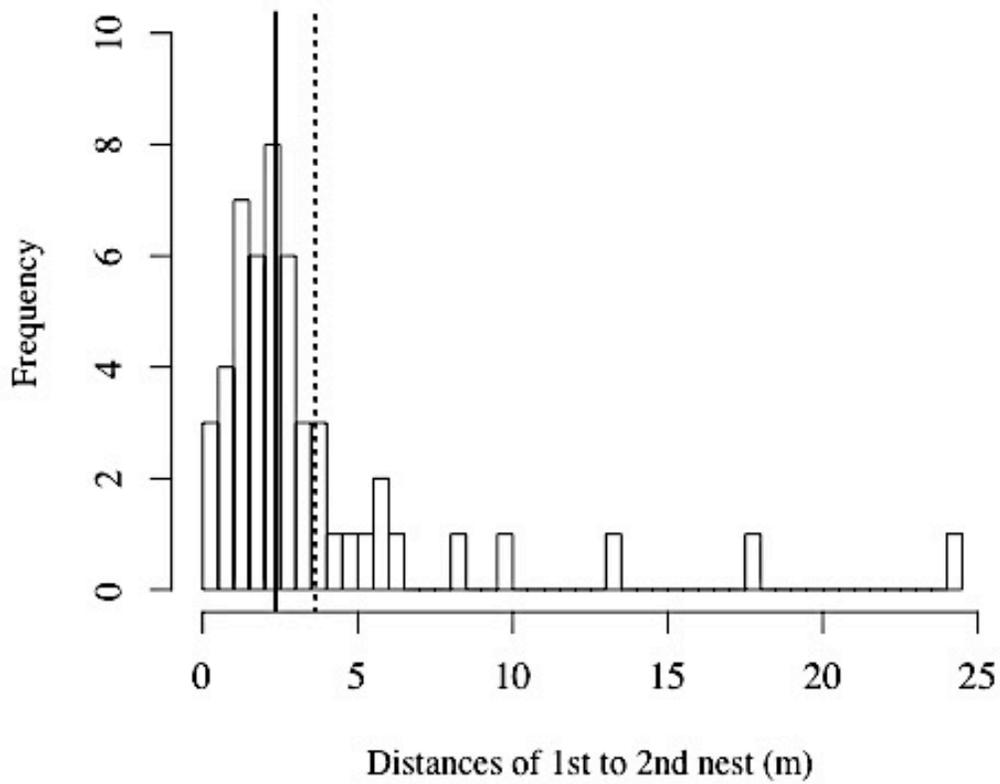
Figure A5. Frequency of the distances moved between the first and second nest in meters at one site, Colorado Horse Rescue (CHR), for the years of 2010 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 2.35 m, mean = 3.63 m, sd = 4.33 m, n = 51).
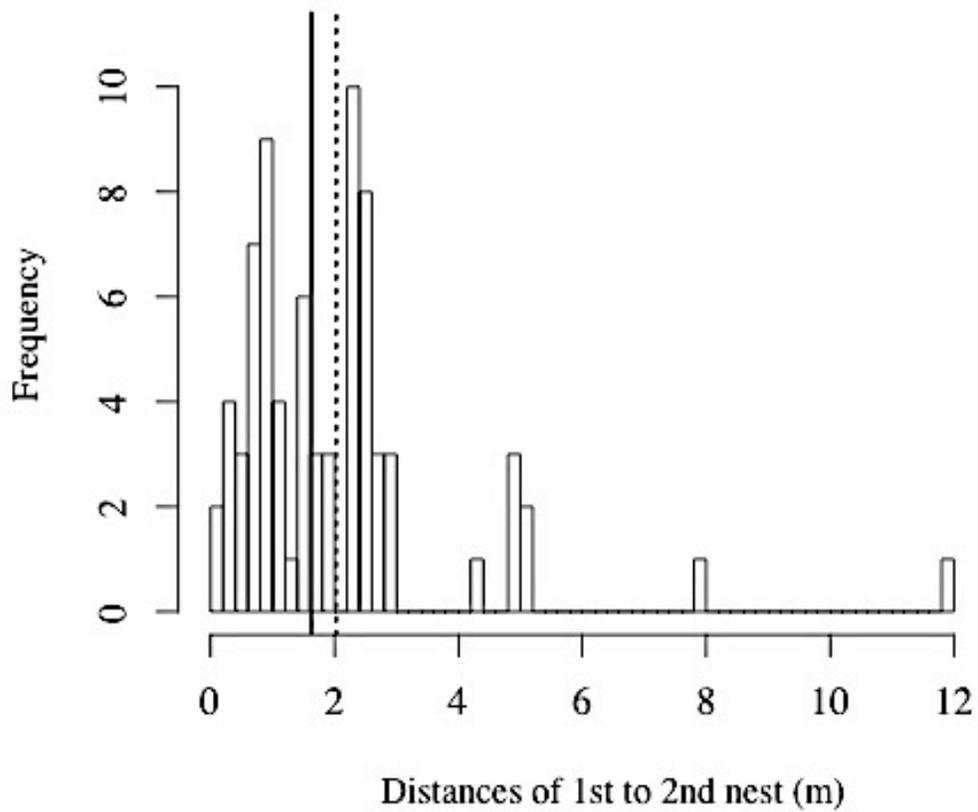
Figure A6. Frequency of the distances moved between the first and second nest in meters at one site, Golden Grizzly (GG), for the years of 2009 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 1.62 m, mean = 2.02 m, sd = 1.83 m, n = 74).
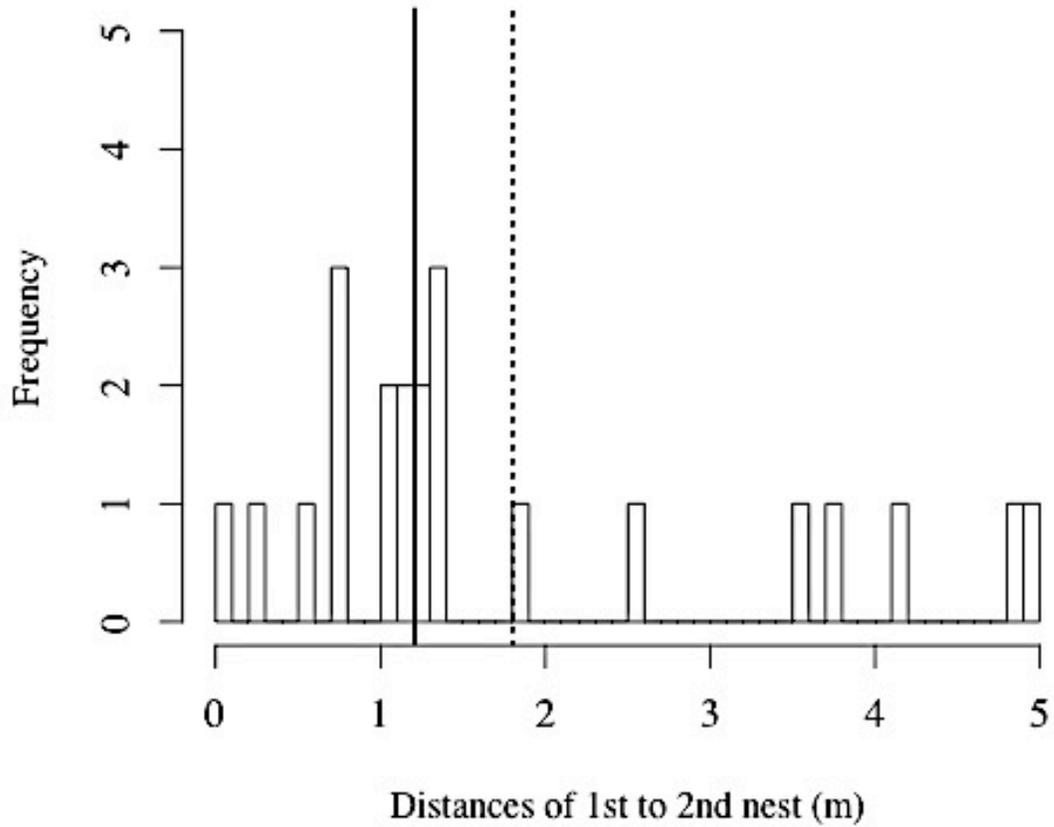
Figure A7. Frequency of the distances moved between the first and second nest in meters at one site, Make Believe (MB), for the years of 2008 to 2014. The solid black line represents the median distance and the dotted line represents the mean (median = 1.21 m, mean = 1.80 m, sd = 1.48 m, n = 22).

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