CORRELATES AND FITNESS CONSEQUENCES OF NATAL DISPERSAL IN SWAINSON'S HAWKS

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Abstract. Natal dispersal is an important, yet often poorly studied, process in population ecology. Natal dispersal can affect population structure and individual fitness. We examined correlates of natal dispersal distances of a population of Swainson's Hawk (*Buteo swainsoni*) in northern California that has been monitored from 1979 to 2010. We examined the effects of sex, number of offspring fledged, population density, primary productivity around a nest site, and annual trends on dispersal from the natal site to the breeding site of individuals recruited into the breeding population. Female Swainson's Hawks dispersed farther than males. Natal dispersal was negatively correlated with primary productivity and was positively correlated with population density around the nest site. We found no correlation between natal dispersal distance and lifetime reproductive success of those individuals recruited into the breeding population, indicating no fitness costs of increased dispersal. We examined the potential genetic contributions to dispersal distance by examining differences in dispersal distance between full siblings. We found that the dispersal difference between siblings was significantly more similar than would be expected by chance. However, we detected no relationships between paternal or maternal natal dispersal distances and natal dispersal of offspring, although sample sizes were limited. We conclude that observed similarities in siblings' natal dispersal distance were likely a result of similarities in unmeasured environmental variables rather than of a genetic mechanism of natal dispersal. Perinatal conditions seemed to have significant effects on distances offspring dispersed, but increased natal dispersal had no apparent consequences on fitness.

Key words: Buteo swainsoni, *fitness, lifetime reproductive success, territory quality.*

Correlatos y Consecuencias en la Adecuación Biológica de la Dispersión Natal en *Buteo swainsoni*

Resumen. La dispersión natal es un proceso importante, aunque usualmente poco estudiado, en ecología de poblaciones. La dispersión natal puede afectar la estructura de la población y la adecuación biológica individual. Examinamos los correlatos de las distancias de dispersión natal de una población de *Buteo swainsoni* en el norte de California que ha sido monitoreada desde 1979 hasta 2010. Examinamos los efectos del sexo, número de pichones que dejaron el nido, densidad poblacional, productividad primaria alrededor de un sitio de nidificación y tendencias anuales en la dispersión desde el sitio natal al sitio de cría de individuos reclutados en la población reproductora. Las hembras de *B. swainsoni* se dispersaron más lejos que los machos. La dispersión natal se correlacionó negativamente con la productividad primaria y se correlacionó positivamente con la densidad poblacional alrededor del sitio de nidificación. No encontramos una correlación entre la distancia de dispersión natal y el éxito reproductivo de toda la vida de aquellos individuos reclutados en la población reproductora, indicando que no hay un costo en la adecuación biológica dado por un incremento en la dispersión. Examinamos las contribuciones genéticas potenciales a la distancia de dispersión examinando las diferencias en la distancia de dispersión entre las crías hermanas. Encontramos que la diferencia de dispersión entre los hermanos fue significativamente más similar que lo que se esperaría por azar. Sin embargo, no detectamos relaciones entre las distancias de dispersión natales paterna o materna y la dispersión natal de las crías, aunque los tamaños de muestreo fueron limitados. Concluimos que las similitudes observadas en la distancia de dispersión natal entre crías hermanas fueron probablemente el resultado de similitudes en variables ambientales no medidas más que un mecanismo genético de dispersión natal. Las condiciones perinatales parecen tener efectos significativos en las distancias de dispersión de las crías, pero un aumento en la dispersión natal no tuvo consecuencias aparentes en la adecuación biológica.

INTRODUCTION

Natal dispersal, here defined as the distance moved from birthplace to breeding territory, may be fundamental to the population ecology (Lidicker 1975) and genetic structure of a species (Ehrlich and Raven 1969). However, it is often not well studied in natural populations, and its effects on individuals' fitness are generally poorly understood (Greenwood 1980). Natal conditions may play a large role in the distance offspring disperse and subsequent fitness of offspring, (e.g., by being recruited into a higher-quality breeding territory; Newton and Marquiss 1983, Arcese 1989, Byholm et al. 2003). Individuals may avoid fitness costs by limiting dispersal (e.g., Murray 1967, Greenwood 1980, Waser 1985). Therefore, it is important to investigate how perinatal conditions affect distance of dispersal of offspring to their new territories as well as the potential effects on fitness of dispersal distance.

Several factors have been thought to play a role in natal dispersal. First, the natal-dispersal hypothesis suggests natal dispersal may be integral to avoiding inbreeding (Dobson and Jones 1985, Johnson 1986, Pusey 1987). In fact, natal dispersal often tends to be farther in one sex, decreasing the potential for siblings to mate (Clarke et al. 1997, Forero et al. 2002, Pasinelli et al. 2004). In addition, optimizing outbreeding may increase overall fitness (Shields 1982). Other factors, such as territory quality, may influence natal dispersal. For example, individuals that fledge from higher-quality sites disperse less, which may result from those individuals trying to recruit into a higher-quality breeding site (Newton and Marquiss 1983, Brown and Brown 1992, Spear et al. 1998).

In contrast, the resource-competition hypothesis suggests that individuals in areas with increased competition for resources or nesting sites should disperse farther to reduce intraspecific competition (Greenwood et al. 1979, Waser 1985, Nilsson 1989). Thus individuals of species with high survival and philopatry to breeding sites (i.e., species with little predicted change in successive years) should disperse farther to attempt to find areas of lower population density, thereby reducing competition for resources.

It is also unclear how genetics may play a role in natal dispersal. While it has long been hypothesized that there could be a genetic component (Howard 1960, Greenwood et al. 1979, Newton and Marquiss 1983), few studies have quantitatively analyzed environmental versus genetic components of natal dispersal (but see Forero et al. 2002, Pasinelli et al. 2004). If there is a genetic component to natal dispersal, we would predict that siblings of the same sex should disperse similar distances.

Fitness costs related to dispersal are hypothesized to come from a number of factors, such as increased costs of movement, an inability to use resources effectively, or a reduced knowledge of predators (Johnson and Gaines 1990). Despite the hypothesized costs of natal dispersal (e.g., Bengtsson 1978, Greenwood 1980), the consequences of varying dispersal distances are unclear. Some evidence has shown that individuals that disperse farther recruit at older ages (Spear et al. 1998), reproduce at a lower rate (Newton and Marquiss 1983), or even have lower lifetime production of fledglings (Pasinelli et al. 2004). However, the current evidence for fitness consequences related to dispersal are equivocal (e.g., Arcese 1989).

We examined potential genetic correlations of natal dispersal and effects of varying dispersal distances on fitness in Swainson's Hawk (*Buteo swainsoni*). Distances of natal dispersal of Swainson's Hawks can be large, with some individuals traveling 320 km from their natal site to their breeding territory (England et al. 1997). Generally, however, individuals disperse considerably shorter distances. In a previous study of this population, Woodbridge et al. (1995) found that natal dispersal was 8.2 km (range 0–18.1 km) with no significant differences between males and females.

We predicted that natal dispersal should be inversely correlated with measures of territorial quality, with individuals fledging in good condition recruiting closer to natal territories of higher quality (Arcese 1989, Byholm et al. 2003). Conditions of the natal territory can affect an individual's fitness (Briggs et al., unpubl. data), so we predict a positive correlation between the quality of the natal and breeding habitat, as individuals that fledge from high-quality sites should also be of relatively high quality and thus be able to compete for higher-quality breeding sites.

METHODS

Surveys for Swainson's Hawks breeding the Butte Valley of California (41° 49′ N, 122° 0′ W) began in 1979. During these initial surveys, breeding adults were trapped and marked with unique plastic numeric color bands to identify each bird individually; nestlings were banded with U.S. Geological Survey (USGS) metal bands. Nestlings that were later recruited into the breeding population were then trapped and given an additional unique color band. Hawks were trapped with a dho-gaza with a Great Horned Owl (*Bubo virginianus*) as a lure (Bloom et al. 1992) or a bal-chatri with a mouse or sparrow as a lure. Partial surveys continued in the valley through 1986. In 1987, the surveys were expanded to include a census of the population of the entire valley floor. The population was monitored intensively through the late 1990s. From 1999 to 2010 the survey effort varied with the number and experience of field technicians; however, each year we attempted to census the valley floor completely. Despite variation in survey effort, we have not observed any differences by habitat type in probability of detection of individuals (Briggs 2007).

Surveying the valley floor by vehicle and on foot, we observed adults during the breeding season for signs of mating behavior (e.g., undulating flight, copulation, nest building). The high density of roads, facilitated by the agricultural nature of the valley, allowed much of the surveying to be from vehicles, which helped minimize disturbance of breeding pairs. Once we

identified a pair we observed it until we located its nest. To avoid nest abandonment we did not approach nest trees until a week after the mean date of hatching (June 16) (Woodbridge 1991). We banded nestlings at ≥3 weeks of age, but in most years of the study, to limit time spent at the nest site, did not age and measure most of them. We considered chicks fledged once they had reached at least 80% of the age at fledging (Steenhof 1987) and individuals recruited when they were caught in subsequent years or their aluminum band was read through a spotting scope.

Using digital ortho quarter-quads with a 1-m resolution, we calculated natal dispersal distance in ArcMAP 9.3 by plotting nest locations. Natal dispersal distance was calculated as the distance from the natal site to the site where an individual was first recorded breeding, identified by behavior (e.g., copulation, nest building, nest defense). If a recruited individual was trapped and could not be assigned to a nest site it was excluded from this analysis.

We assessed territory quality by productivity and occupancy. A territory's productivity was the average number of fledglings produced per attempted nest over the course of the study (Newton 1989, Sergio and Newton 2003). Therefore, if a territory was not located or was unoccupied in a given year, we excluded that year from the calculation of the territory's average productivity. The second method used the proportion of years a territory was occupied. We summed the number of years a territory was occupied once it was first discovered, giving an overall occupancy rate (Newton 1989). As the population has grown since the beginning of the study (Briggs 2007), we could not simply divide the number of years a territory was occupied by the number of years in the study, because some territories were not discovered until many years later, and new territories are discovered almost every year. Therefore we instead counted the number of years once a territory was initially discovered and used the proportion of years a territory was occupied once it was first discovered active, providing a metric of territory quality.

We used a surrogate of prey availability as a measure of annual differences in territory quality. As our study area is in the Great Basin ecoregion (Franklin and Dyrness 1973), irrigated crops, particularly alfalfa, provide a good index of prey availability (Woodbridge 1991, Whisson et al. 1999). The normalized differential vegetation index (NDVI) measures the overall greenness of a landscape (i.e., the quantity of chlorophyll) and can be considered an index of primary productivity (Chen and Brutsaert 1998). We calculated the NDVI by using Landsat 4 or 5 imagery from the USGS for all scenes in which data were available (i.e., where cloud cover allowed for a clear view of the study area). To average each territory's NDVI each year, we took the average NDVI value within 500 m of the nest site in each scene in which information was available, then averaged these values over the breeding season (i.e., May–August).

STATISTICAL ANALYSES

To correct for bias arising from incomplete sampling of the study area, we used a modified version of the method of Baker

et al. (1995) and Sharp et al. (2008) to estimate natal dispersal. Briefly, we estimated a dispersal distribution and found that a gamma distribution described dispersal distance for both males and females, and we calculated separate curves for each sex. From this distribution we generated 50 000 dispersal distances for both males and females. We randomly generated a dispersal direction from a uniform distribution from a randomly chosen nest location observed within the study area. From that we calculated the recruits' potential breeding site. We excluded points that fell within unsuitable habitat and generated a new dispersal distance and directions until we simulated 50 000 dispersals. We defined unsuitable habitat as areas with pine- or fir-dominated forest >2 km from open sagebrush, agriculture, or lakes. We then calculated the number of dispersals outside the study area and calculated probability of detection of dispersal. We then corrected for observation bias to create an unbiased estimate of natal dispersal (Baker et al. 1995).

We examined relationships between conditions at the nest site and natal dispersal distance by regressing natal site quality (i.e., both average fledging number and occupancy rate), year fledged, number of nestlings, NDVI within 500 m of the nest site, habitat quality, and average distance to the 3 nearest neighbors (i.e., an index of nest density) against the log-transformed natal dispersal distance. We used the log of natal dispersal distance to help normalize residuals of the regression. We used a generalized linear mixed model (GLMM) using the lme4 package (Bates and Maechler 2009) in R 2.10.1 (R Development Core Team 2009) to account for potential pseudoreplication by including year of the study and natal site as random factors in the analysis. We used Akaike's information criterion (AIC) to assess model fit (Akaike 1973), using model weights to calculate model-averaged regression estimates, and calculating the sums of the model weights (Σw_i) to assess the relative importance of each variable (Burnham and Anderson 2002). Higher Σw_i indicates greater proportional representation in the top models and higher support for a given model term.

We used a GLM in R 2.10.1 to regress lifetime reproductive success (LRS) against the log-transformed dispersal distance for both males and females. We used a quasi-Poisson distribution to account for overdispersion of LRS (i.e., variance was greater than the mean). We censored individuals observed within the last 3 years of the study and those known to have been missed for ≥2 years over the course of study to exclude individuals whose LRS value was biased low either because of low detection or because the bird was still breeding. Similarly, we regressed quality of the natal territory against that of breeding territory. We measured overall territory quality with a principal components analysis (PCA) of territory occupancy and territory productivity and taking the first principal component as the measure of territory quality. The PCA takes correlated variables and finds a linear combination that reduces the number of variables and eliminates multicollinearity (Zuur et al. 2007). The first principal

component describes most of the variation in highly correlated variables.

Finally, we examined potential genetic contributions to dispersal distance in several ways. First we examined the influence of parents on the dispersal distance of siblings versus that of unrelated young by treating each unique pair as a random effect in a GLMM and assessing model fit. We assigned each pair a unique number each year if the identity of one or both parents was unknown. If young of the same parents dispersed similar distances, the identity of the pair would be a significant predictor of dispersal distance of the young. Next we examined relationships between distances of natal dispersal of breeding adults and their offspring with a GLM regressing natal dispersal distance of offspring against natal dispersal distance of their parents. As males and females may affect their offspring differently, we analyzed the sexes separately. When more than one offspring per breeding male was recruited, we used the average value of his offspring to regress against the parental dispersal distance. We performed the same procedure for breeding females. Finally, in cases where we knew the natal dispersal distances of both parents and their recruited offspring we averaged the natal dispersal distance of the parents and regressed it against that of the offspring. All results are given as means ± SE.

RESULTS

Over the 32 years of the study we trapped 117 breeding Swainson's Hawks that were originally banded as nestlings (i.e., had a known natal dispersal distance). Three individuals that were banded and fledged outside the study area were detected breeding in the study area, and one individual fledging in the study area was detected breeding outside the study area. The mean productivity of a territory was 1.38 ± 0.03 fledglings for all territories over the course of the study, and average territory occupancy across the study was 0.51 ± 0.02. The average territory has been monitored for 17.5 ± 0.7 years.

Natal dispersal ranged from 0.1 to 28.0 km for males ($n = 71$) and from 0.2 to 46.0 km for females ($n = 46$). The mean natal dispersal distance of females (11.1 ± 1.1 km) was significantly greater than that of males (8.3 ± 0.7 km; $\Sigma w_i = 1.0$; Fig. 1; Table 1). Unbiased estimates of natal dispersal were 9.5 km and 15.1 km for males and females, respectively.

There was a negative relationship between dispersal distance and primary productivity around the nest site (i.e., NDVI; $\Sigma w_i = 1.0$) and strong evidence of an interaction between sex and primary productivity, with females from more productive territories recruiting closer to the natal site than males (Fig 2; $\Sigma w_i = 1.0$). There also was a strong negative correlation between the average distance of the closest three nearest neighbors and natal dispersal distance ($\Sigma w_i = 1.0$). For example, when average nearest-neighbor distance decreased by 1000 m, average natal dispersal increased by 150 m.

The first principal component of the PCA of territory occupancy and territory productivity explained 91% of
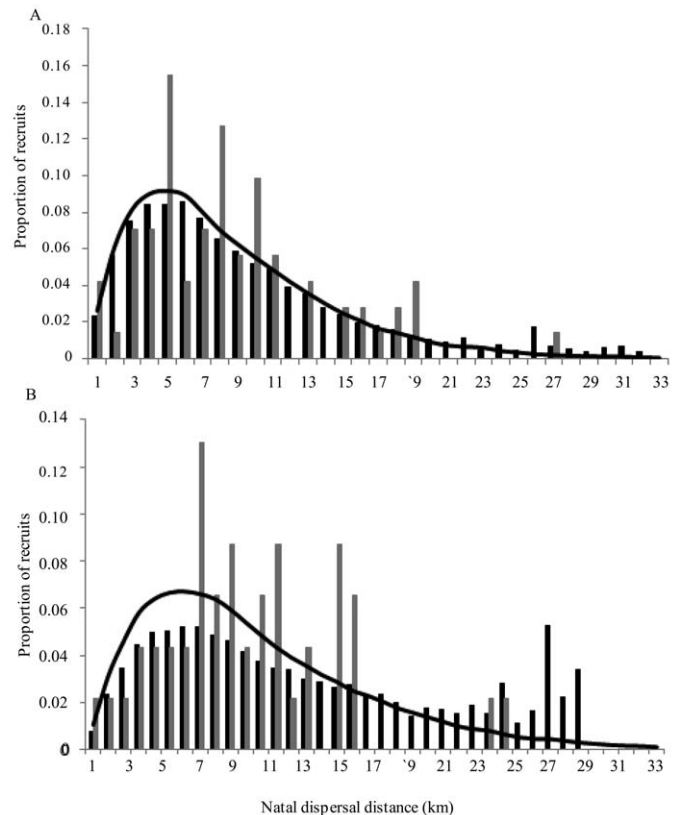

FIGURE 1.   Distances dispersed by male (A) and female (B) Swainson's Hawks from their natal site to their first breeding site in Butte Valley, California, 1979–2010. Gray bars, observed distances; black bars, distances corrected for bias (see text). The solid line is the gamma distribution used to approximate the distribution of natal dispersal.

the variation of the two variables. There was no correlation between quality of natal territory and breeding territory of recruited offspring in either site occupancy ($P = 0.16$, $n = 117$) or site productivity ($P = 0.56$, $n = 117$). Similarly, there was no correlation between LRS (mean = 6.0 ± 0.7) and dispersal distance for males ($n = 35$, $P = 0.29$) or females ($n = 29$, $P = 0.32$).

TABLE 1.   Relative fit of models to the distance of natal dispersal of Swainson's Hawks banded from 1979 to 2010 in Butte Valley, California.

Model[a]	ΔAIC	w_i	Deviance
Sex × PP + DNN	0[b]	0.63	185.5
Sex + PP + DNN	1.2	0.35	186.8
Sex + fledge + PP + DNN	6.7	0.02	186.6
Sex + PP	14.2	0.00	219
Sex + fledge + PP + DNN + year	14.9	0.00	186.5

[a]Variables are offspring sex, primary productivity (PP), average distance of 3 nearest neighbors (DNN), number of fledglings (fledge) produced and year of fledging (year); w_i is the Akaike weight of the model (Burnham and Anderson 2002).
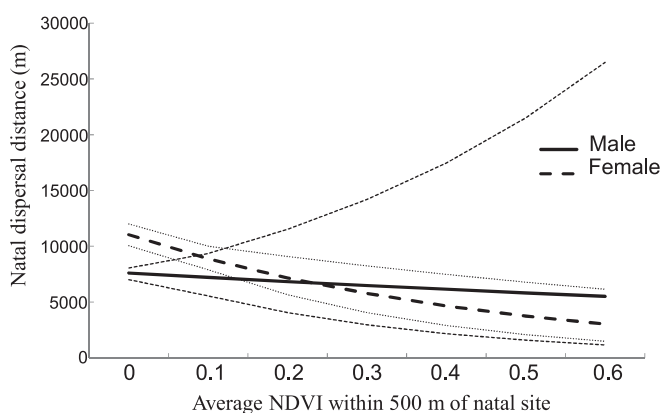[b]Minimum value of AIC = 219.0.

FIGURE 2. Distance dispersed by male and female Swainson's Hawks from their natal site to their first breeding site in Butte Valley, California, in relation to the average primary productivity (measured by NDVI) within 500 m of their natal site. Thin dashed lines represent 95% confidence interval for males, dotted lines that for females.

Of parents that recruited >1 fledgling we observed 64 offspring from 25 unique parental pairs. Differences in dispersal distance between siblings (2665 ± 275 m) were significantly lower than those between unrelated young (7894 ± 533 m). There was strong evidence that a pair's identity predicted dispersal distances of their young, and the AIC score from adding identity of the pair was 68.1 AIC units lower than that in the best model without it (Table 1). In contrast, there was no correlation between maternal ($n = 11$) dispersal and dispersal of either male or female offspring ($P = 0.85$ and 0.86, respectively). Neither in our GLM was there a correlation between paternal ($n = 17$) natal dispersal and average natal dispersal of offspring for male or female offspring ($P = 0.47$ and 0.64, respectively; Fig. 3A). Similarly, there was no correlation between average natal dispersal of parents and that of their offspring ($n = 5$, $P = 0.70$; Fig. 3B).
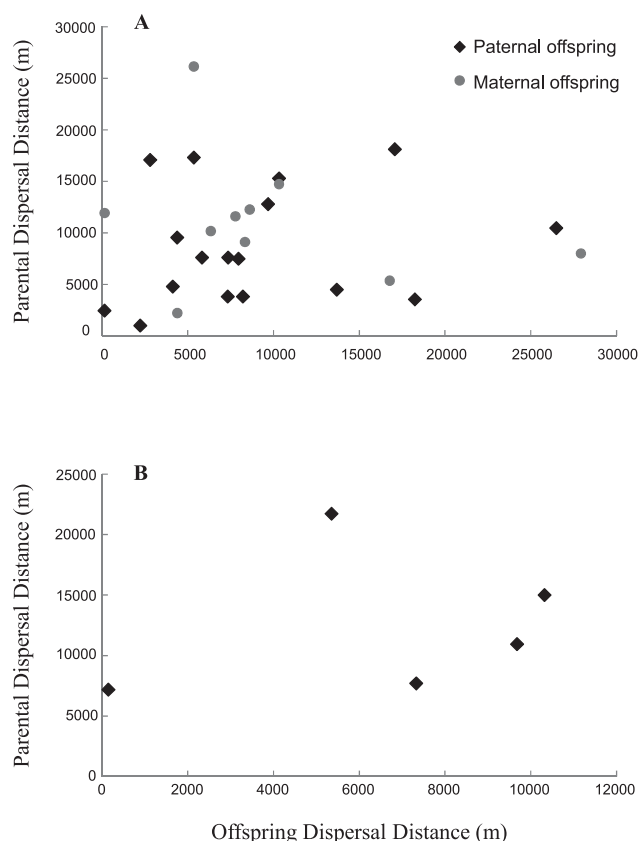

FIGURE 3. Relationship between (A) paternal (black diamonds) and maternal (gray circles) dispersal distances from natal site to breeding site and the average distance of their offspring's dispersal from natal site to breeding site for Swainson's Hawks breeding in Butte Valley, California, 1979–2010. There were no significant relationships between natal dispersal of parents and of offspring. (B) Average natal dispersal of both mother and father compared to the average natal dispersal of their offspring.

DISCUSSION

We found significant correlations between conditions at a natal site and dispersal distance within our study area. Increased primary productivity correlated well with individuals, particularly females, dispersing closer to their natal site. Evidence for males recruiting closer to the nest site because of higher primary productivity of the natal territory was considerably more equivocal. As primary productivity in this area is correlated with abundance and availability of prey (C.W.B., unpubl. data; Woodbridge 1991), it is reasonable to suspect that females prefer to nest closer to natal sites with more prey abundance or better habitat (Arcese 1989, Byholm et al. 2003), especially when high-quality habitat is spatially clumped, as it is in our study area (Woodbridge 1991). Nest survival is higher in areas with high NDVI (C.W.B., unpubl. data). Thus, for females in a spatially heterogeneous environment, recruiting closer to high-quality sites may be a strategy to maximize LRS and fitness. In contrast, males may try to recruit as close

as possible to their natal site in any case so that increases in natal primary productivity have relatively little effect on their ability to recruit closer to that site.

When comparing dispersal distances of siblings, we found strong evidence of positive correlations between dispersal distances of siblings, which suggests a genetic component of natal dispersal distance (Forero et al. 2002). In parent/offspring regressions, however, we found no correlations between natal dispersal distances of parents and those of offspring, regardless of the metric used (i.e., maternal effects, paternal effects, or average parental effects), suggesting that there is no significant genetic component of natal dispersal in Swainson's Hawk. The species' high fidelity to breeding sites (Woodbridge et al. 1995) means that nestlings of the same pair are likely to be reared in similar conditions. Although we were able to find substantial correlations within territories and among siblings, it seems more likely that the relationship between siblings arises as a result of our inability to adequately describe the characteristics

of a site that influence dispersal. If we could determine other environmental factors influencing dispersal distance we should be able to remove the correlation of siblings' dispersal distance.

Although an experiment involving swapping offspring between nests is necessary to disentangle environmental from parental/genetic effects on dispersal distance rigorously, our results demonstrate it is unlikely that such an experiment would find a simple genetic component of dispersal in this species. Rather, interactions of genotype with the environment may play a role in dispersal decisions of offspring. This is evidenced by the lack of parent–offspring relationships in dispersal distance that we would expect from a simple genetic component. These results call for caution when only siblings are used to examine the influences of genetics on natal dispersal distances. Forero et al. (2002) compared dispersal distances of siblings and unrelated young, found a significant correlation between siblings, and concluded it was evidence of genetic determination of dispersal distance. However, our results suggest that environmental variation, rather than genetics or avoidance of inbreeding, is the primary driver of correlations in natal dispersal distances within a brood. Although dispersal distances of siblings raised in different years were similar, these results may be explained by offspring experiencing similar environmental conditions, as a result of the high site fidelity of breeding adults (Woodbridge et al. 1995). Thus when only siblings raised in a similar environment are compared, observed correlations may be due to unmeasured environmental variation rather than to inheritance.

Like those of other studies that examine recruitment of offspring, our analyses are subject to problems due to the limited spatial scale of the study area. Our analyses may be biased because of our inability to detect individuals outside the study area. We know that some individuals disperse outside the study area (Woodbridge et al. 1995) and that individuals from outside the study area have immigrated into the area, so emigration from the population may not be insignificant. In other parts of their breeding range Swainson's Hawks have been observed dispersing as much as 320 km (England et al. 1997). Thus the correlation we demonstrate may not entirely represent the true relationships with dispersal, and our conclusions are limited because of the limited scope and nature of our study area and our inability to reliably detect individuals outside the study area. However, we cannot determine the number of individuals that emigrated or the distance they emigrated. We also could not test for effects of date of hatching on this population because for most of the study these data were unavailable.

While we were unable to account for individuals that dispersed outside the study area, it is notable that we still found patterns in dispersal distance, particularly in males, for which our estimate of unbiased natal dispersal was similar to the observed distance. Because of several factors, however, fitness costs may occur at scales greater than the one we could measure. First, there may indeed be no correlation between the quality of natal and breeding sites, meaning that in Swainson's Hawk, in which

the period of parental care is much shorter than the period in which a bird is a juvenile or subadult (England et al. 1997), an individual's quality may not be inherited genetically or socially.

Contrary to results published previously on this population (Woodbridge et al. 1995), we found sex differences in natal dispersal distances, with females dispersing an average of 5.6 km farther than males over the course of the study. The disparity in results is likely a function of sample size. Since this population has grown since the beginning of the study (Briggs 2007), increasing from 31 nests in 1986 at the time of the first census to 84 nests in 2010, it is possible that this difference may have arisen in response to the population's growth and increased density (i.e., density-dependent dispersal). However, we did not find interaction between sex and year of the study ($\Sigma w_i = 0.0$) or an interaction between sex and nearest-neighbor distance ($\Sigma w_i = 0.0$), so we do not believe this is likely. In contrast, individuals that fledged in areas where the nearest neighbors were closer tended to disperse farther, providing support for the concept of density-dependent dispersal (Greenwood et al. 1979, Nilsson 1989). While we attempted to find all nests in the study area each year beginning in 1986, we are unlikely to have been completely successful in any given year because of logistic constraints and an inability to access some private lands. For example, in 2010 we located 84 nests and suspected 5 additional nests not confirmed because of land-access issues. Thus average distances between neighbors may be biased high. This bias is likely to be small in most years because of Swainson's Hawk's conspicuous behavior and preference for open habitats. Despite potential noise in the dataset, we found a strong correlation between natal dispersal and distance of the nearest neighbor to the natal nest.

While the relationship between number of offspring produced and dispersal distance can be positive and related to habitat quality (Stacey and Ligon 1987, Pärt 1991) or negative to avoid inbreeding (Pusey 1987), we found no correlation between number of offspring fledged and the distance of natal dispersal of those offspring. This result provides evidence that natal dispersal may not be related to avoidance of inbreeding, as individuals from nests producing more offspring should disperse farther to avoid mating with siblings (Pärt 1991).

Despite spatial limitations due to the constraints of the study area we were able to find significant differences between natal dispersal distances of Swainson's Hawks according to conditions of the natal habitat. Specifically, we found a correlation between females' natal dispersal distance and primary productivity of the natal site. In addition, we found that Swainson's Hawk follows a pattern like that of many other bird species with females dispersing farther than males.

ACKNOWLEDGMENTS

LITERATURE CITED

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle, p. 267–281. *In* B. N. Petrov and F. Csaki [EDS.], Second international symposium on information theory. Akademiai Kiado, Budapest.

ARCESE, P. 1989. Intrasexual competition, mating system and natal dispersal in Song Sparrows. Animal Behaviour 38:958–979.

BAKER, M. B., N. NUR, AND G. R. GEUPEL. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wrentits. Condor 97:663–674.

BATES, D., AND M. MAECHLER [ONLINE]. 2009. lme4: Linear mixed-effects models using S4 classes. <http://cran.r-project.org/web/packages/lme4/index.html> (18 February 2010).

BENGTSSON, B. 1978. Avoiding inbreeding: at what cost? Journal of Theoretical Biology 73:439.

BLOOM, P. H., J. L. HENCKEL, E. H. HENCKEL, J. K. SCHMUTZ, B. WOODBRIDGE, J. R. BRYAN, R. L. ANDERSON, P. J. DETRICH, AND T. L. MAECHTLE. 1992. The dho-gaza with Great Horned Owl lure: an analysis of its effectiveness in capturing raptors. Journal of Raptor Research 26:167–178.

BRIGGS, C. W. 2007. Survival and nesting ecology of Swainson's Hawks in Butte Valley, CA. M.Sc. Thesis, University of Nevada, Reno, Reno.

BROWN, C. R., AND M. B. BROWN. 1992. Ectoparasitism as a cause of natal dispersal in Cliff Swallows. Ecology 73:1718–1723.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York.

BYHOLM, P., P. SAUROLA, H. LINDÉN, AND M. WIKMAN. 2003. Causes of dispersal in Northern Goshawks (*Accipiter gentilis*) in Finland. Auk 120:706–716.

CHEN, D., AND W. BRUTSAERT. 1998. Satellite-sensed distribution and spatial patterns of vegetation parameters over a tallgrass prairie. Journal of the Atmospheric Sciences 55:1225–1238.

CLARKE, A. L., B. E. SÆTHER, AND E. RØSKAFT. 1997. Sex biases in avian dispersal: a reappraisal. Oikos 79:429–438.

DOBSON, F. S., AND W. T. JONES. 1985. Multiple causes of dispersal. American Naturalist 126:855–858.

EHRLICH, P. R., AND P. H. RAVEN. 1969. Differentiation of populations. Science 165:1228–1232.

ENGLAND, A. S., M. J. BECHARD, AND C. S. HOUSTON. 1997. Swainson's Hawk (*Buteo swainsoni*), no 265. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

FORERO, M. G., J. A. DONAZAR, AND F. HIRALDO. 2002. Causes and fitness consequences of natal dispersal in a population of Black Kites. Ecology 83:858–872.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. Department of Agriculture, Forest Service, Portland, OR.

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.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63:152–161.

JOHNSON, C. N. 1986. Sex-biased philopatry and dispersal in mammals. Oecologia 69:626–627.

JOHNSON, M. L., AND M. S. GAINES. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449–480.

LIDICKER, W. Z. 1975. The role of dispersal in the demography of small mammals, p. 103–128. *In* F. B. Golley, K. Petrusewicz and L. Ryskowski [EDS.], Small mammals: their productivity and population dynamics. Cambridge University Press, Cambridge, England.

MURRAY, B. G. 1967. Dispersal in vertebrates. Ecology 48:975–978.

NEWTON, I., AND M. MARQUISS. 1983. Dispersal of Sparrowhawks between birthplace and breeding place. Journal of Animal Ecology 52:463–477.

NEWTON, I. 1989. Lifetime reproduction in birds. Academic Press, New York.

NILSSON, J. Å. 1989. Causes and consequences of natal dispersal in the Marsh Tit, *Parus palustris*. Journal of Animal Ecology 58:619–636.

PÄRT, T. 1991. Philopatry pays: a comparison between Collared Flycatcher sisters. American Naturalist 138:790–796.

PASINELLI, G., K. SCHIEGG, AND J. R. WALTERS. 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. American Naturalist 164:660–669.

PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution 2:295–299.

R DEVELOPMENT CORE TEAM. 2009. R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.

SERGIO, F., AND I. NEWTON. 2003. Occupancy as a measure of territory quality. Journal of Animal Ecology 72:857–865.

SHARP, S. P., M. B. BAKER, J. D. HADFIELD, M. SIMEONI, AND B. J. HATCHWELL. 2008. Natal dispersal and recruitment in a cooperatively breeding bird. Oikos 117:1371–1379.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany, NY.

SPEAR, L. B., P. PYLE, AND N. NUR. 1998. Natal dispersal in the Western Gull: proximal factors and fitness consequences. Journal of Animal Ecology 67:165–179.

STACEY, P. B., AND J. D. LIGON. 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.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity, p. 157–190. *In* B. A. G. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [EDS.], Raptor management techniques manual. Scientific Technical Series 10, National Wildlife Federation, Washington, DC.

WASER, P. M. 1985. Does competition drive dispersal? Ecology 66:1170–1175.

WHISSON, D. A., S. B. ORLOFF, AND D. L. LANCASTER. 1999. Alfalfa yield loss from Belding's ground squirrels in northeastern California. Wildlife Society Bulletin 27:178–183.

WOODBRIDGE, B. 1991. Habitat selection by nesting Swainson's Hawk: a hierarchical approach. M.Sc. thesis, Oregon State University, Corvallis, OR.

WOODBRIDGE, B., K. K. FINLEY, AND P. H. BLOOM. 1995. Reproductive performance, age structure, and natal dispersal of Swainson's Hawks in the Butte Valley, California. Journal of Raptor Research 29:187–192.

ZUUR, A. F., E. N. IENO, AND G. M. SMITH. 2007. Analyzing ecological data. Springer, New York.