Biology Faculty Publications and Presentations        Department of Biological Sciences

8-1-2013

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# LOCAL RECRUITMENT AND NATAL DISPERSAL DISTANCES OF AMERICAN KESTRELS

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*Abstract.* Variation in recruitment patterns and dispersal behavior can have important consequences for population viability, genetic structure, and rates of evolutionary change. From 1992 to 2006 we studied a marked population of American Kestrels (*Falco sparverius*) nesting in boxes in southwestern Idaho to identify factors that affect local recruitment and natal dispersal distances. A low proportion (4%) of locally produced kestrels (*n* = 2180) returned to nest in study area boxes. Offspring of locally produced individuals were 3.1 times more likely to return than offspring of parents that did not hatch in study area boxes and, independent of a parent's origin, males were 1.8 times more likely than females to return. Kestrels that hatched earlier in the breeding season and those that hatched immediately prior to a mild winter were more likely to return. Local natal dispersal distances were best explained by sex and parental origin but not by hatching dates. Fifty-four males moved an average of 5.3 km from their natal box to the location of their first breeding in the study area, and 27 females moved an average of 9.8 km. Offspring of locally produced parents dispersed shorter distances within the study area than offspring of other parents, and local natal dispersal distances of locally produced parents correlated with those of their same-sex offspring. Patterns of natal dispersal of American Kestrels in southwestern Idaho appear to be driven by a combination of parental dispersal tendencies and ecological factors. The population consists of a mix of immigrants and philopatric birds.

*Key words:* **American Kestrel, dispersal,** Falco sparverius, *recruitment.*

## Reclutamiento Local y Distancias de Dispersión Natal de *Falco sparverius*

*Resumen.* La variación en los patrones de reclutamiento y el comportamiento de dispersión pueden tener consecuencias importantes para la viabilidad poblacional, la estructura genética y las tasas de cambio evolutivo. Desde 1992 a 2006 estudiamos una población marcada de individuos de *Falco sparverius* que anidan en cajas en el sudoeste de Idaho para identificar los factores que afectan el reclutamiento local y las distancias de dispersión natal. Una baja proporción (4%) de individuos producidos localmente (*n* = 2180) regresaron a anidar a las cajas del área de estudio. Las crías de los individuos producidos localmente tuvieron una probabilidad 3.1 veces mayor de regresar que las crías de padres que no eclosionaron en las cajas del área de estudio e, independientemente del origen de los padres, los machos tuvieron una probabilidad 1.8 veces mayor que las hembras de regresar. Los individuos que eclosionaron más temprano en la estación reproductiva y aquellos que eclosionaron inmediatamente antes de un invierno moderado presentaron una mayor probabilidad de regresar. Las distancias de dispersión natal local fueron mejor explicadas por el sexo y el origen parental pero no por la fecha de eclosión. Cincuenta y cuatro machos se desplazaron un promedio de 5.3 km desde su caja natal a la localización de su primera reproducción en el área de estudio, y 27 hembras se desplazaron un promedio de 9.8 km. Las crías de los individuos producidos localmente se dispersaron distancias más cortas dentro del área de estudio que las crías de otros padres y las distancias de dispersión natal local de los padres producidos localmente se correlacionaron con aquellas de sus crías del mismo sexo. Los patrones de dispersión natal de *F. sparverius* en el sudoeste de Idaho parecen estar condicionados por una combinación de tendencias de dispersión parental y factores ecológicos. La población consiste en una mezcla de aves inmigrantes y filopátricas.

## INTRODUCTION

The probability of a bird returning to nest in its natal region depends on factors that affect survival until the first nesting season as well as dispersal behavior. Recruitment of locally produced birds ("local recruitment" as defined by Verboven and Visser 1998) has important implications for population trends, maintenance of genetic variation, and local adaptation (Matthysen et al. 2001, Haché and Villard 2010). Weather conditions, especially in winter, can affect probabilities of young birds' survival by increasing energetic costs (Root 1988) or reducing food availability (Romanowski and Żmihorski 2009). The probability of local recruitment may be related to date of hatching. For example, European Sparrowhawks (*Accipiter nisus*) and Great Tits (*Parus major*) that hatch early in the season have a higher probability of recruiting to the local

population (Newton and Marquiss 1984, Verboven and Visser 1998). Birds hatched early in the season may have higher survival rates because of high-quality parents (Nooker et al. 2005, Hipfner et al. 2010), greater access to resources (Hipfner et al. 2010), a prolonged post-fledging period, or some combination of these factors. In some species, post-fledging survival of young that fledge early tends to be higher (Naef-Daenzer et al. 2001), and young raptors that fledge early in the season also have more time to gain the skills and stamina (Newton 1979, Sherrod 1983) needed to survive a harsh winter or long migration.

Dispersal behavior has an important effect on population dynamics and the genetic composition of populations. The distance an animal moves from its birth place to its first breeding site (natal dispersal) influences the distribution, dispersion, and density of populations and is often determined by the costs of dispersing relative to the costs of staying on or near the natal territory (natal philopatry; Greenwood 1980). Dispersal behavior is likely determined by a combination of ecological, social, and genetic factors (Hansson et al. 2003, Pasinelli et al. 2004). Dates of hatching also may affect dispersal because resident birds produced early in the season may have the opportunity to establish territories before birds hatched later in the season (Nilsson 1989, Ellsworth and Belthoff 1999). Recent studies suggest that in some species of birds the level of heritability of dispersal is high (Doligez et al. 2009, Charmantier et al. 2011). Evidence for heritability comes from resemblance between siblings and between parent and offspring in propensity to disperse and distance of dispersal (Massot and Clobert 2000, Doligez and Pärt 2008, Doligez et al. 2009). Selective pressures for natal dispersal or philopatry may differ by sex (Greenwood 1980, Clarke et al. 1997, Perrin and Mazalov 2000). Female birds typically disperse farther than males because most birds have a mating system based on resource defense in which males defend resources to attract females (Greenwood 1980, Arlt and Pärt 2008).

Most studies of dispersal underestimate dispersal distances and probably do not reflect the population as a whole because animals that disperse outside the study area are unlikely to be detected (Koenig et al. 2000, Doligez and Pärt 2008, Morrison and Wood 2009). Scale issues often preclude testing hypotheses about underlying causes of dispersal. Nevertheless, information on dispersal distances within a study area ("local" dispersal distances) can provide important insights about dispersal patterns, especially those of related individuals.

The American Kestrel (*Falco sparverius*) is a small, socially monogamous, and sexually dimorphic raptor that occurs throughout North and South America (Smallwood and Bird 2002). It is common in habitats used and modified by humans, and, as a secondary cavity nester, it readily uses nest boxes. Males defend territories and provide most of the food for females during courtship, incubation, and early brood rearing; both parents provide food to nestlings >10 days of age (Balgooyen 1976). Kestrels of migratory populations establish territories and select mates in the first few weeks after arrival on the breeding grounds (Bortolotti and Iko 1992), but in resident populations yearling males may acquire territories as early as the autumn of their hatching year (Smallwood and Smallwood 1998; Steenhof, unpubl. data). Previous studies of natal dispersal in the American Kestrel have been short-term or based on small sample sizes (Bowman et al. 1987, Jacobs 1995, Miller and Smallwood 1997). None have reported natal dispersal distances of related individuals.

The objectives of this study were to clarify factors that affect natal dispersal and recruitment of locally produced individuals. From 1992 to 2006 we studied a marked population of American Kestrels nesting in boxes in southwestern Idaho, where the nesting season is prolonged (March–August). In this area the kestrel is a partial migrant; some birds migrate as far as Mexico (Steenhof and Peterson 2009a), while others remain on the breeding grounds year round (Henny and Brady 1994, Steenhof and Peterson 2009a; Heath and Steenhof, unpubl. data). We hypothesized that factors related to survival and dispersal should affect local recruitment and that the probability of local recruitment should be higher for kestrels hatched earlier in the nesting season and in years following mild winters. We hypothesized that the kestrel should be similar to most other birds and show sex-biased dispersal, with males being more likely to return to breed in their natal region and dispersing shorter distances from their natal boxes than females. We also hypothesized that local natal dispersal distances may be influenced by parental traits such as parental origin and reproductive timing. We predicted that offspring of locally produced parents should be more likely to return and disperse shorter distances than offspring of nonlocal parents and that birds hatched earlier in the breeding season should disperse shorter distances than those hatched later.

## METHODS

### STUDY AREA

The southwestern Idaho study area (43° N, 116° W) included nest boxes that had been erected 1–6 years before the study began. Approximately 20% of boxes were on the backs of highway signs along Interstate 84, 20% were on trees in rural residential properties near Kuna, Idaho, and 60% were on wooden poles in agricultural and exurban areas south of Boise and Meridian, Idaho. The irregularly shaped study area (65 km × 22 km) consisted mainly of open agricultural and rangeland habitat and encompassed approximately 1000 km². During the study period, land-use patterns changed, and the number of housing developments increased. The number of boxes available to kestrels each year varied from 90 to 126, with the numbers gradually decreasing over time (Steenhof and Peterson 2009b), as boxes were destroyed by vandals or developers. Each nest box could be considered a "nesting territory" as defined by Newton and Marquiss (1982), in that it represented a confined locality where kestrels nested and

where no more than one pair bred at one time. During the study, the kestrel population was stable or slightly increasing (Steenhof and Peterson 2009a). The percent of boxes occupied by kestrels increased over time (fig. 4 in Steenhof and Peterson 2009a), averaging 48% each year (range 20–74%). In addition to our nest boxes, kestrels had opportunities to nest in old trees and buildings as well as boxes erected by others within and on the periphery of our study area.

DATA COLLECTION

In March of each year from 1992 to 2006, we checked, cleaned, and added fresh wood shavings to all boxes. Some boxes were replaced and repaired each year. We revisited all boxes in late April, late May, and early June to check for kestrel occupancy. We removed nests of the European Starling (*Sturnus vulgaris*) to keep all boxes suitable for kestrel nesting. We revisited boxes with kestrel eggs or young as often as necessary to capture adults, age and band young, and ascertain nesting success and number of young produced (Steenhof and Peterson 2009a). We captured incubating adults by blocking the box's entrance with a hole-stuffer and then, while standing on a ladder, manually removing the bird from the box. During brood-rearing, we used a mist net with a live Great Horned Owl (*Bubo virginianus*) as a lure to capture adults we had not been able to catch during incubation, (Steenhof et al. 1994). Approximately 90% of the females and 70% of the males nesting in boxes were captured each year (Steenhof and Peterson 2009b). We placed numbered aluminum bands on all nestlings produced in nest boxes when they were 23–25 days of age and on all adults captured.

We aged young by a photographic key (Griggs and Steenhof 1993) and, on the basis of the estimated ages of nestlings, assigned median hatching dates to all broods. To account for variation by year in hatching dates, we computed an adjusted hatching date by dividing the median hatch date for a brood by the median hatch date for all broods in the year of hatching. We considered a pair to be successful when their young reached 80% of fledging age (75% feathered or approximately 22 days; Griggs and Steenhof 1993).

We considered birds hatched and marked as nestlings in our boxes to be locally produced, and we distinguished locally produced parents from parents that were first captured and marked as nesting adults in our analyses of parental origin. Our sample of individuals "not locally produced" likely included some unmarked birds produced just outside the study area and some produced in natural cavity nests within the study area. If this misclassification was common, it would have decreased our ability to detect an effect of parental origin. We assumed that adults trapped at boxes were the parents of the young in boxes. The frequency of extra-pair copulations in the American Kestrel is low (Villarroel et al. 1998), and brood parasitism has never been documented in the species (Smallwood and Bird 2002). We had no evidence for

trios (e.g., Towers 1990), so it is likely that nearly all adults were the true genetic parents of the eggs and young that they tended. We used the origin of an offspring's same-sex parent (i.e., fathers of males and mothers of females) to examine the effects of parental origin in all analyses (Pasinelli et al. 2004).

We determined Universal Transverse Mercator coordinates of boxes with topographic maps or the Global Positioning System. We defined natal dispersal distance as the straight line distance between the nest box where a kestrel hatched and the box where it was first known to nest. We also calculated all possible distances between each box and report the range of possible dispersal distances, distribution shape, and value of the third quartile. To represent the severity of a winter, we used the sum of "heating" degree days (DD) recorded December through February at the study area's northern boundary (http://www.wunderground.com/history/). Degree days are calculated by summing the difference between hourly temperatures and a threshold (18.3 °C) and dividing the sum by the number of hours. Degree days are considered a reliable index of the amount of energy required to heat a mass (Saino et al. 2011) and have been used to estimate thermal accumulation in plants (Roundy et al. 2007) and seasonal shifts in the timing of avian migration (Saino et al. 2011). Winters with high DD were more severe than winters with low DD. In winters with higher DD, birds may experience a higher energetic demand for thermoregulation (Ardia 2002), or they may migrate farther from the breeding area (Visser et al. 2009, Heath et al. 2012). .

STATISTICAL ANALYSES

We used generalized linear mixed models (GLMM) fit by Laplace approximation (Bolker et al. 2009) with a binomial distribution and logit link to examine whether parental origin, sex, adjusted hatching date, or severity of the winter (indexed by DD) affected the probability that a locally produced kestrel would survive and return to the nesting population. We did not assess the effect of age on local recruitment because most kestrels (84%) nested in their first year after hatching (Steenhof and Heath 2009), and older age classes were poorly represented in the dataset. We selected GLMMs instead of apparent-survival models in Mark because our interest in random variables outweighed our concern for bias in probability of recapture. We used quantile–quantile plots of residuals from the most parsimonious GLMM compared to residuals from a simulated model with normally distributed error (1000 replicates) to assess whether our model met assumptions (Rhodes et al. 2009). We used a linear mixed model (LMM) fit by maximum likelihood (Bolker et al. 2009) to evaluate the effects of sex, adjusted hatching date, and parental origin on local natal dispersal distances. We did not assess the effect of severity of the winter on dispersal distance because we assumed that inclement winter weather affects survival more than local dispersal patterns. To avoid pseudoreplication, we

included brood identity as a random effect in the GLMM and LMM (Bolker et al. 2009) because siblings may not represent independent experimental units (Ferrer 1993, Dale 2010, Doligez et al. 2012). To improve convergence and allow effect sizes to be compared more easily, we standardized adjusted hatching date and DD by subtracting the mean from each observation and dividing by the standard error of the variable (Rhodes et al. 2009). Candidate models included all possible additive models of the predictor variables (Doherty et al. 2012). We examined correlations between predictor variables to check for issues with multicollinearity. We used an information-theoretic approach in our analyses of local recruitment and dispersal distances and evaluated support for candidate models with Akaike's information criterion (AIC; Burnham and Anderson 2002, Rhodes et al. 2009). We considered models with $\Delta$AIC < 2.0 as good candidate models and calculated model-averaged parameter estimates and unconditional standard errors for the final model across all models (Burnham et al. 2011). To be consistent with the information-theoretic framework of the analysis, we calculated 85% confidence intervals for each parameter estimate (Arnold 2010). We also calculated cumulative AIC weights for each variable by summing the weights from all models that contained a given predictor variable (Burnham and Anderson 2002).

We evaluated the similarity of natal dispersal distances of locally produced parents and their offspring with a simple correlation analysis. We did not include parental dispersal distance in our linear mixed model of natal dispersal distance because we did not have dispersal distances of parent birds that had not been raised in study area boxes. We compared the distributions of male and female dispersal distances with the distribution of all possible distances between nest boxes by a Kolmogorov–Smirnov goodness-of-fit test.

We log-transformed all dispersal distances for statistical analysis (Newton and Marquiss 1983). Values reported under Results are means ± SD, and all null hypothesis tests were evaluated for significance at $P \leq 0.05$. We used R (version 2.14.0, R Development Core Team 2011) and SAS (version 9.2, SAS Institute 2008) for statistical analyses.

## RESULTS

### PROBABILITY OF RETURNING

Of 2180 kestrels banded as nestlings from 1992 to 2005, 81 (4%) were later encountered as adults nesting in boxes within the study area. Parental origin was the most important predictor of hatch-year birds surviving and returning to breed in the study area (cumulative $w = 0.97$, Table 1). Male and female kestrels were 3.1 times more likely to return if their fathers or mothers, respectively, had hatched in study area boxes ($\beta = 1.12$, 85% CI: 0.56–1.7) than were offspring of parents first marked as adults. Males were 1.8 times more likely to return than females (5% of 1113 males vs. 3% of 1067 females;

cumulative $w = 0.82$, $\beta = 0.60$, 85% CI: 0.13–1.06, Table 1). Date of hatching had a negative effect on the probability of returning ($\beta = -0.30$, 95% CI: −0.57 to −0.02; cumulative $w = 0.68$); individuals that hatched earlier in the year were more likely to return to breed than those that hatched later. The severity of the preceding winter had a negative effect on the probability that a bird would return ($\beta = -0.29$, 95% CI: −0.58 to −0.01; cumulative $w = 0.66$); birds were less likely to return after colder winters (winters with high DD). Recruits came from 70 out of 528 broods (13% of all broods). Two recruits each were produced from 11 of the 70 broods so that 22 of 81 recruits (27%) were siblings.

None of the nestlings we banded during the study were recaptured or recovered outside the study area during the breeding season. Locally produced males constituted 16–35% (mean = 25 ± 7%) of the males nesting in boxes each year from 1998 to 2006, and locally produced females constituted 2–10% (mean = 6 ± 3%). From 1998 to 2006, 51 of 292 males encountered nesting in boxes for the first time (17%) had been banded as nestlings, and 20 of 360 females encountered nesting for the first time (5%) had been banded as nestlings in the study area.

### NATAL DISPERSAL DISTANCES

Males that returned to nest in the study area moved an average of 5.3 km from their natal box to their first nesting location in

TABLE 1. Predictor variables, difference in AIC from the top model ($\Delta_i$), model weights ($w_i$), deviance, and standard deviation of the intercept for the random effect of brood identity (Brood_id) used to predict whether an American Kestrel hatched in southwestern Idaho returned to nest. Table includes all models with $w_i > 0.01$ and the intercept-only model. Predictor variables include parental origin (whether the same-sex parent was locally produced: parent_org), sex (male), adjusted hatching date (adjHatD), and degree days (DD) as a measure of the severity of the preceding winter.

| Model | $\Delta_i$[a] | $w_i$ | Deviance | SD[b] |
|---|---|---|---|---|
| Parent_org + sex + adjHatD + DD + (Brood_id) | 0.0 | 0.37 | 652.3 | 1.5 |
| Parent_org + sex + adjHatD + (Brood_id) | 1.4 | 0.18 | 655.7 | 1.5 |
| Parent_org + sex + DD + (Brood_id) | 1.7 | 0.16 | 656.0 | 1.5 |
| Parent_org + sex + (Brood_id) | 2.8 | 0.09 | 659.1 | 1.6 |
| Parent_org + adjHatD + DD + (Brood_id) | 3.0 | 0.08 | 657.3 | 1.4 |
| Parent_org + DD + (Brood_id) | 4.5 | 0.04 | 660.8 | 1.5 |
| Parent_org + adjHatD + (Brood_id) | 4.5 | 0.04 | 660.8 | 1.5 |
| Parent_org + (Brood_id) | 5.6 | 0.02 | 663.9 | 1.5 |
| Sex + adjHatD + DD + (Brood_id) | 6.4 | 0.01 | 660.7 | 1.6 |
| Intercept only (Brood_id) | 16.8 | 0.00 | 677.1 | 1.7 |

[a]Minimum AIC is 664.3.
[b]Standard deviation of the intercept for random effect of brood identity.

the study area (median = 3.8 km, range 0.8–24.1 km, $n$ = 54, SD = 4.7). Females moved an average of 9.8 km (median = 8.2 km, range 2.6–42.9 km, $n$ = 27, SD = 9.0). Distances between available boxes ranged from 0.18 km to 65 km and had a positive skew with most (75%) distances less than 21 km. More than 80% of male and female kestrels we banded as nestlings and recaptured as breeding adults nested in their first year after hatching (Steenhof and Heath 2009). Six females marked by other investigators as nestlings moved an average of 11.6 km from their natal boxes to nest in boxes in our study area (median = 11.2, range 6.7–19.9 km, SD = 4.7). Two males marked by other investigators as nestlings moved 8.4 and 132.7 km from their natal boxes to nest in boxes in our study area. We included all birds except the long-distance immigrant in subsequent analyses of distances moved, whenever appropriate information was available. We also included a female marked as a nestling in the study area in 1990 that nested in a study area box in 1992.

Of 55 males with known local natal dispersal distances, 62% nested within 5 km of their natal box, whereas only 26% of 34 females nested within 5 km (Fig. 1). No females nested within 2.5 km of their natal box, compared to 27% of males. The distribution of males' ($D$ = 0.63, $P$ < 0.001) and females' ($D$ = 0.44, $P$ < 0.001) dispersal distances differed significantly from the distribution of nest box distances, indicating that dispersal distances did not simply reflect box arrangement. Although no individual returned to nest in its natal box in the first year it nested, two males returned to nest in their natal boxes in their third and fourth years. One male returned to his father's natal nesting box, making his natal dispersal distance identical to his father's.

A linear mixed model based on a reduced dataset of birds with known hatching dates and parental origin showed
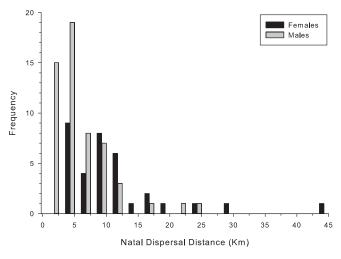


FIGURE 1. Frequency distribution of local natal dispersal distances for 55 male and 34 female American Kestrels in southwestern Idaho, 1990–2006.

TABLE 2. Predictor variables, difference in AIC from the top model ($\Delta_i$), model weights ($w_i$), deviance, and standard deviation of the intercept for the random effect of brood identity (Brood_id) used to predict natal dispersal distances of American Kestrels in southwestern Idaho. Table includes all models with $w_i$ > 0.01 and the intercept-only model. Predictor variables include parental origin (whether the same-sex parent was locally produced: parent_org), sex (male), and adjusted hatching date (adjHatD).

| Model | $\Delta_i$[a] | $w_i$ | Deviance | SD[b] |
|---|---|---|---|---|
| Parent_org + sex + (Brood_id) | 0.0 | 0.67 | 19.5 | 0.2 |
| Parent_org + sex + adjHatD + (Brood_id) | 1.9 | 0.26 | 19.1 | 0.2 |
| Sex + (Brood_id) | 5.3 | 0.05 | 27.2 | 0.2 |
| Sex + adjHatD + (Brood_id) | 7.6 | 0.01 | 27.2 | 0.2 |
| Parent_org + (Brood_id) | 8.9 | 0.01 | 30.7 | 0.2 |
| Intercept only (Brood_id) | 16.7 | 0.00 | 40.8 | 0.2 |

[a]Minimum AIC was 30.4.
[b]Standard deviation of the intercept for random effect brood identity.

that local dispersal distances of kestrels were associated with both sex (cumulative $w$ = 0.99) and parental origin (cumulative $w$ = 0.94; Table 2). Males ($n$ = 48) dispersed shorter distances than did females ($n$ = 25; β = –0.23, 85% CI: –0.33 to –0.14), and kestrels produced by parents raised in study area boxes dispersed shorter distances than did birds produced by other parents (β = –0.22, 85% CI: –0.34 to –0.11). The evidence for an effect of hatching date on local dispersal distance (cumulative $w$ = 0.27) was low compared to the evidence for the effects of sex and parental origin. The parameter estimate and associated confidence interval for hatching date suggested that this variable had a small and inconsistent effect on local natal dispersal distances (β = –0.02, 85% CI: –0.07–0.03) and was not predictive of local dispersal distance.

Natal dispersal distances of young correlated closely with those of their parents, especially for fathers and sons (Table 3). Dispersal distances of mothers and daughters also correlated positively and significantly, on the basis of a very small sample. But there was no correlation between natal dispersal distances of fathers and daughters or of mothers and sons (Table 3).

TABLE 3. Pearson's correlation coefficient ($r$), sample size ($n$), and $P$-values demonstrating similarity of natal dispersal distances for American Kestrels and their offspring in southwestern Idaho.

| | $r$ | $n$ | $P$ |
|---|---|---|---|
| Father/son | 0.62 | 17 | 0.008 |
| Father/daughter | –0.08 | 7 | 0.870 |
| Mother/son | 0.33 | 4 | 0.670 |
| Mother/daughter | 0.96 | 4 | 0.045 |
| All parents/offspring | 0.44 | 32 | 0.012 |

DISCUSSION

The estimated proportion of nestlings that returned to nest in study area boxes was <5%, similar to rates recorded for other migratory open populations (Korpimäki and Lagerström 1988, Brown and Roth 2002). Low return rates reflect rates of both emigration and mortality. None of the kestrels we marked as nestlings was recovered >43 km from its natal box during a subsequent breeding season. Young that dispersed outside our study area were not likely to be detected even though other investigators were capturing nesting kestrels in other parts of southwestern Idaho. An analysis of continental banding data indicated that 15% of male and 26% of female American Kestrels recovered in the first breeding season after they hatched were >100 km from their natal sites; one male dispersed more than 2000 km from his natal area to the place he settled in his first breeding season (Gonzalez 1986). The fact that locally produced birds constituted less than 20% of the population nesting in Idaho boxes suggests that the kestrel is similar to other bird species in which external recruitment is extensive (Lambrechts et al. 1999, Martin et al. 2000).

Mean number of territories traversed within the study area was 5 or 6 for males and 10 or 11 for females, depending on whether we considered a territory's diameter to be 1 km (Miller and Smallwood 1997) or 0.9 km, based on nearest-neighbor distances between boxes. The number of territories traversed equates to Shields' (1983) effective dispersal distance, and on the basis of a threshold of 10 indicates that males are highly philopatric and females are marginally philopatric, supporting previous findings that kestrels are loosely philopatric (Bowman et al. 1987).

FACTORS INFLUENCING RECRUITMENT
AND DISPERSAL

*Dispersal of related individuals.* Patterns of American Kestrels' dispersal in southwestern Idaho were associated with parental dispersal tendencies. We found evidence for similar dispersal tendencies in parents and offspring at two scales. Offspring of locally produced individuals were more likely to return to nest in the study area than were offspring of parents that did not hatch in study area boxes, and kestrels produced by parents raised in study area boxes dispersed shorter distances within the study area than did birds produced by other parents. A young kestrel's dispersal behavior was related to the behavior of its parent of the same sex (fathers for males and mothers for females), and the association appeared to be stronger in males than in females, as in the Red-cockaded Woodpecker (*Picoides borealis;* Pasinelli et al. 2004). Local natal dispersal distances of male kestrels correlated positively with those of their sons, as did those of mothers and daughters. Resemblance of parents and offspring in propensity to disperse can arise from a genetic component, early parental effects, or a shared environment (Massot and Clobert 2000, Doligez and Pärt 2008). Previous studies have documented

similar patterns of dispersal of sibling raptors (Newton and Marquiss 1983, Ferrer 1993, Forero et al. 2002), but these results are often confounded by the fact that siblings disperse from the same location, and it is difficult to isolate the effects of inheritance from those of environmental conditions and landscape patterns (van Noordwijk 1984, Massot and Clobert 2000, Matthysen et al. 2005, Dale 2010). In our study, parent kestrels and their offspring had similar dispersal patterns but dispersed from different boxes in different years, suggesting that either genetics or early parental effects (and not location) were important determinants of dispersal behavior (Hansson et al. 2003, Pasinelli et al. 2004).

*Sex-biased dispersal.* Within the study area, female kestrels dispersed significantly farther than males, and they were less likely to return to nest in study area boxes. Our findings are consistent with Greenwood's (1980) predictions. Sex-biased dispersal is thought to be associated with a resource-defense system in which males defend territories and females select mates (Greenwood 1980, Miller and Smallwood 1997). The sex that defends the territory and its resources should be more philopatric, and the sex that selects the mate should be more likely to disperse. For birds that nest in cavities, the nest site is an important resource that may affect an individual's success in mating and subsequent nesting. Our findings contrast with Miller and Smallwood's (1997) finding of no difference in natal dispersal distance between the sexes of a different subspecies of the American Kestrel in Florida at a similar local scale. However, the kestrels we studied were similar to the European Sparrowhawk (Newton and Marquiss 1983), Merlin (*Falco columbarius*; James et al. 1987), Cooper's Hawk (*Accipiter cooperii*; Rosenfield and Bielefeldt 1992), Peregrine Falcon (*Falco peregrinus*; Restani and Mattox 2000), and Black Kite (*Milvus migrans*; Forero et al. 2002), in which juvenile females disperse farther than males. Dispersal of male kestrels may be discontinuous, as in males of the White-tailed Ptarmigan (*Lagopus leucurus*; Martin et al. 2000) and Red-cockaded Woodpecker (Kesler et al. 2010). In Wisconsin, Jacobs (1995) found that median dispersal distances of young female American Kestrels were greater than those of males, but a male dispersed 362 km, farther than any of the females (Jacobs 1995). The male that immigrated 133 km into our study area supports the idea that most males stay close to their natal areas, but those that disperse may move farther than most females.

*Seasonal effects.* Our finding that birds hatched earlier in the season were more likely to survive and return to nest than were birds hatched later in the season is consistent with studies of the Great Tit (Verboven and Visser 1998), Wood Thrush (*Hylocichla mustelina*; Brown and Roth 2002), Peregrine Falcon (Restani and Mattox 2000), European Sparrowhawk (Newton and Marquiss 1984), and other populations of the American Kestrel (Smallwood and Smallwood 1998). Early hatching dates may reflect high-quality parents (Nooker et al. 2005, Hipfner et al. 2010) or more access to food resources (Hipfner et al. 2010). Alternatively, birds that hatch early simply may

have more time to develop hunting and other skills before the onset of winter. Migratory individuals should be in better condition at the time of migration (Arroyo et al. 2002), increasing their probability of survival. In resident populations, early-hatched birds, particularly males, should have an advantage in finding and competing for territories near their natal areas (Smallwood and Smallwood 1998). The probability of returning may be related to a tendency for early-hatched birds to disperse shorter distances, but we found no evidence for this tendency in the American Kestrels we studied. Hatching date has been positively associated with dispersal distance in songbirds competing for nesting territories (Nilsson 1989), but not in the European Sparrowhawk (Newton and Marquiss 1983).

*Severity of winter.* American Kestrels in southwestern Idaho, like female European Sparrowhawks in northern Denmark (Millon et al. 2009), had a higher probability of returning to nest in the study area after warmer winters. Mild winters may favor increased over-winter survival within the study area because of reduced energetic costs, increased prey availability, or both. Alternatively, warm winters may be associated with an increased proportion of birds that overwinter in the study area in any particular year. American Kestrels tend to migrate shorter distances in warmer winters (Heath et al. 2012). Overwintering kestrels that do not undertake long-range movements may be less likely to nest outside the natal region, and they avoid the risks and energetic costs of migration.

*Implications.* Recruitment patterns are important for populations experiencing rapid change of regional land use or climate. A high and constant flow of immigrants from different environments may affect a population's ability to respond to changing local conditions. Our data suggest that the American Kestrel population in southwestern Idaho consists of a mix of dispersers and a core group of philopatric individuals. According to Hansson et al. (2003) the persistence of multiple strategies for dispersal is evolutionarily stable in species inhabiting heterogeneous environments. In our sudy area, weather and changing land-use patterns contributed to annual variation and spatial heterogeneity in prey availability (Steenhof and Peterson 2009a). Our results are consistent with the prediction that annual variation in the environment favors dispersal, whereas spatial variation favors philopatry (Johnson and Gaines 1990). Tendencies for both philopatry and dispersal will likely continue to coexist within this population and should enhance the species' ability to adapt to changing environments (Hannson et al. 2003).

## ACKNOWLEDGMENTS

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