The Auk 127(3):671–677, 2010
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Printed in USA.

SEX-RELATED DISPERSAL IN THE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*)

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Abstract.—The rapid multiclutch mating system of the Mountain Plover (*Charadrius montanus*) provides an opportunity to examine sex differences in natal, within-year, and between-year breeding dispersal. We used nest locations over a 14-year period from a population of Mountain Plovers breeding on prairie dog colonies in Montana to examine sex-related patterns in natal and within-year breeding dispersal. Additionally, we modeled between-year dispersal distances in relation to sex, previous nest fate, and the occurrence of sylvatic plague in the colonies. We also modeled successive nest fate using dispersal distance and these same covariates. We found no evidence of sex differences in distances moved during natal dispersal (mean = 13.0 km for 16 males; mean = 10.2 km for 22 females) or within-year breeding dispersal (mean = 2.8 km for 22 males; mean = 3.0 km for 26 females). The mean (± SE) dispersal distance was 2.7 ± 0.60 km (n = 115) for males nesting in consecutive years and 4.3 ± 0.87 km (n = 87) for females. Previous nest fate was the only factor that had a strong effect on between-year breeding dispersal. On average, birds that were previously successful moved 3.0 ± 0.55 km (n = 149), whereas unsuccessful birds moved 4.6 ± 1.18 km (n = 53). None of the effects tested was suitable for predicting subsequent nest fate. Our work provides a better understanding of dispersal in an uncommon shorebird, additional insight into a novel mating system, and a basis for testing theories of avian dispersal. *Received 30 June 2009, accepted 25 January 2010*

Key words: *Charadrius montanus*, dispersal, Mountain Plover, nest fate, rapid multiclutch, shorebird.

Dispersión Relacionada con el Sexo en *Charadrius montanus*

Resumen.—El sistema de apareamiento rápido y con nidadas múltiples de *Charadrius montanus* brinda una oportunidad para examinar las diferencias entre sexos en la dispersión natal, la dispersión entre épocas de un año y la dispersión reproductiva entre años. Usamos ubicaciones de nidos a lo largo de un período de 14 años de una población de *C. montanus* que se reproduce en colonias de perros de la pradera en Montana para examinar los patrones relacionados con el sexo en la dispersión natal y en la dispersión reproductiva dentro de un año. Además, modelamos las distancias de dispersión entre años en relación con el sexo, el destino previo de los nidos y la presencia de la peste selvática en las colonias. También modelamos el destino sucesivo de los nidos usando la distancia de dispersión y las mismas covariables. No encontramos evidencia de diferencias entre sexos en las distancias de desplazamiento durante la dispersión natal (media = 13.0 km para 16 machos; media = 10.2 km para 22 hembras) ni en las distancias de dispersión reproductiva dentro de un año (media = 2.8 km para 22 machos; media = 3.0 km para 26 hembras). La distancia de dispersión media (± EE) fue de 2.7 ± 0.60 km (n = 115) para los machos que anidaron en años consecutivos y de 4.3 ± 0.87 km (n = 87) para las hembras. El destino previo de los nidos fue el único factor que tuvo un efecto fuerte en la dispersión reproductiva entre años. En promedio, las aves que fueron exitosas previamente se movieron 3.0 ± 0.55 km (n = 149), mientras que las no exitosas se movieron 4.6 ± 1.18 km (n = 53). Ninguno de los efectos probados fue adecuado para predecir el destino subsiguiente de los nidos. Nuestro trabajo provee un mejor entendimiento de la dispersión en un ave playera poco común, perspectivas adicionales sobre un sistema de apareamiento novedoso y una base para poner a prueba teorías sobre la dispersión de las aves.

Much work has been done in the nearly three decades since Greenwood (1980) reviewed mating systems, philopatry, and dispersal in birds, but many of the driving forces behind dispersal are still poorly understood. Several factors are thought to influence a bird's movements, such as previous nest fate, sex of the individual, and habitat quality (Greenwood 1980, Greenwood and Harvey 1982), but the relative importance of these factors differs among studies. Both breeding dispersal (the distance a bird moves between successive nesting attempts) and natal dispersal (the movement from natal location to first breeding site), as defined by Greenwood and Harvey (1982), play roles in population ecology and evolution, including inbreeding avoidance, range expansion, and the ability to colonize novel habitats (Clobert et al. 2001).

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The Auk, Vol. 127, Number 3, pages 671–677. ISSN 0004-8038, electronic ISSN 1938-4254. © 2010 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2010.09059

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One influence on avian natal and breeding dispersal is the individual's sex. Among migratory bird species, males tend to be more philopatric than females (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997), although males tend to be the dispersing sex in waterfowl and sex-role-reversed species (Greenwood and Harvey 1982, Reed and Oring 1993, Clarke et al. 1997). Differences in sex-biased dispersal are usually attributed to variation in the parental roles of the sexes and are thought to be associated with resource or mate defense (Greenwood 1980).

Other work has shown that previous nesting success can also affect avian breeding dispersal. Birds that have previously been successful tend to move shorter distances, have higher return rates, and remain more site-faithful than birds whose nests failed (Haas 1998, Flynn et al. 1999, Hoover 2003, Porneluzi 2003, Sedgwick 2004). This is often referred to as the "decision rule" in the prior-experience hypothesis (Haas 1998, Hoover 2003). However, the effects of previous fate can be confounded by variation between sex and age classes, with females and younger birds being more likely to disperse farther (Payne and Payne 1993).

The Charadriidae include diverse mating systems (Ligon 1999) that offer opportunities to study the roles of sex, prior experience, and habitat change in novel systems. The Mountain Plover (*Charadrius montanus*) is a fairly large (90–110 g) and drably colored member of this family. It has a rapid multiclutch mating system (Graul 1973), an uncommon system in which each member of a pair tends its own nest (Lack 1968; Oring 1982, 1986). Although both male and female Mountain Plovers have similar incubation and chick-rearing responsibilities for their individual nests, it is thought that the males arrive first to the breeding grounds in early to mid-April, establish loose territories, and compete for females (Graul 1973). This is a "resource defense" (rather than "mate defense") system, in which the male digs scrapes and displays within his territory to court females. Hence, females are predicted to be the dispersing sex.

The Mountain Plover has a declining population of 15,000 to 20,000 individuals (Tipton et al. 2009) and is endemic to the Great Plains and Great Basin (Knopf and Wunder 2006). The species breeds in several western states, but >90% of the total population occurs in Montana, Wyoming, and Colorado (Knopf and Wunder 2006). Mountain Plovers in Montana nest primarily on active Black-tailed Prairie Dog (*Cynomys ludovicianus*; hereafter, "prairie dog") colonies (Knowles et al. 1982, Knowles and Knowles 1984, Dinsmore and Knopf 2005), which provide the mix of short vegetation and bare-ground habitat that Mountain Plovers prefer. However, individual prairie dog colonies are subject to outbreaks of sylvatic plague, an epizootic that can completely eliminate a prairie dog colony within the course of a single breeding season (Collinge et al. 2005, Pauli et al. 2006). Within a year, regrowth of vegetation around the burrows renders the colony unsuitable for nesting in the following year. Long-term monitoring of Mountain Plovers in north-central Montana has shown that male-tended nests survived to hatching better than female-tended nests (Dinsmore et al. 2002) but that female-tended broods had higher success than those tended by males (Dinsmore and Knopf 2005).

Previous studies of Mountain Plovers have noted that individuals return to the general area where they had nested previously (Graul 1973; Ellison Manning and White 2001a, b), even to the extent of using the same nest cup (Knopf and Wunder 2006). However, dispersal in this species has not been quantified. Understanding dispersal behavior within this declining population of shorebirds is necessary for evaluating their potential use of available habitat, particularly in relation to the occurrence of sylvatic plague. Our objectives were to (1) examine the influence of sex on natal and within-year breeding dispersal of Mountain Plovers; (2) evaluate the effects of sex, nest fate, and the presence or absence of sylvatic plague at the nesting colony on between-year dispersal; and (3) determine whether the distance moved between successive nesting attempts could be used to predict subsequent nest fate after accounting for the effects of previous nest fate, sex, and occurrence of plague at the previous nesting colony.

Methods

Study area and field data collection.—We studied the dispersal of Mountain Plovers over 14 breeding seasons (1995–2008) in an approximately 3,000-km^2 area located in southern Phillips County in north-central Montana (47°40′–47°55′N, 107°35′–108°30′W), described in detail by Dinsmore et al. (2002). Historically, the disturbance regime included fires and grazing by American Bison (*Bison bison*) and prairie dogs, but it now includes grazing by domestic cattle (*Bos taurus*) and prairie dogs. We studied Mountain Plovers exclusively on prairie dog colonies. Field work began in mid-May and continued until the end of the birds' breeding season, usually late July or early August. Nest searching and monitoring and capture, handling, and banding techniques were similar across years and followed those described by Dinsmore et al. (2002). We individually color-banded adult and hatch-year birds; the latter always remained on their natal colony until fledging. Mountain Plovers are sexually monomorphic, and sex was molecularly determined from feather or blood samples (Avian Biotech International, Tallahassee, Florida) using techniques outlined in Dinsmore et al. (2002). This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol number 5-06-6129-Q.

Spatial data collection and preparation.—Coordinates of all nests were recorded using a Trimble Geo XT handheld global-positioning-system unit running TERRASYNC software (Trimble Navigation, Sunnyvale, California). We mapped active prairie dog colonies by delineating the colony perimeter on the basis of straight-line distances between active burrows. Active burrows were those that had fresh (≤1 week old) droppings, had fresh (≤1 week old) diggings, or harbored ≥1 prairie dog during a visit. Colonies in the study area were mapped every year except 1997, 2003, and 2006. All points and polygons were differentially corrected using PATHFINDER OFFICE software (Trimble Navigation) in Montana State Plane (NAD83) units. Colony centroids were determined by using ARCGIS, version 9.2 (ESRI, Redlands, California), and we calculated the mean centroid for each colony over the entire study period.

To examine natal dispersal in Mountain Plovers, we used data from birds that were banded as chicks and were then found either on a nest ($n = 28$) or tending a brood ($n = 10$) in the study area the following year. If the location of their first nesting attempt was known, we calculated the linear distance between the centroid of the colony where the bird hatched and the coordinates of its first nesting attempt. We also used data from 1-year-old birds that were

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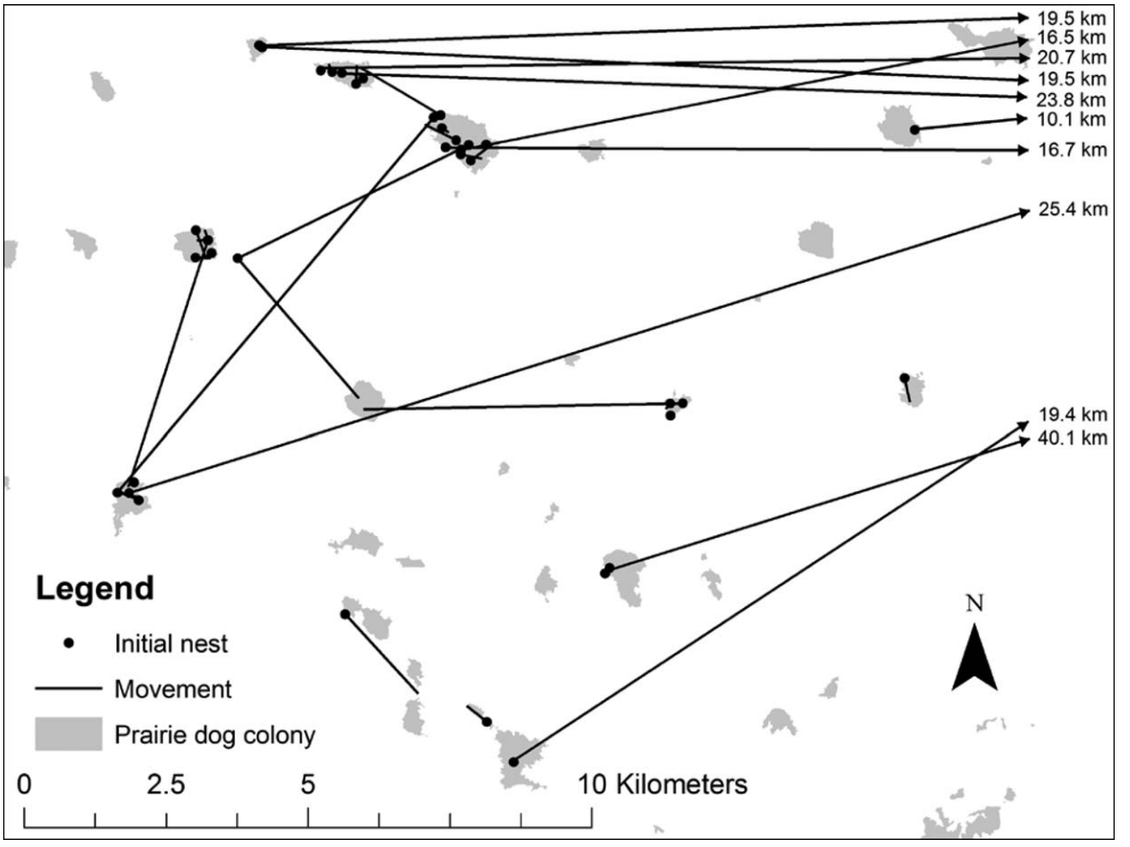

FIG. 1. Typical linear dispersal distances (km) between successive nesting attempts of Mountain Plovers nesting on Black-tailed Prairie Dog colonies in southern Phillips County, Montana, 1995–2008. Note that this map depicts only a small portion of the study area so that individual dispersal movements can be seen more clearly.

found tending a brood on a colony by measuring from the centroid of the colony where they hatched to the centroid of the colony where they brooded young. The largest colony in the study area had a maximum radial distance of 1 km, so the maximum error in nest assignment (vs. colony centroid) is 1 km. For the 10 individuals for which we used this approach, the distances were always <0.5 km.

To evaluate breeding dispersal, we calculated the linear distance between consecutive nesting attempts both within and between years. The within-year movements were obtained for individuals that renested in the study area after their initial nest failed, whereas between-year movements were based on successive nesting attempts in the study area in consecutive years (Fig. 1). All distances were ln-transformed to improve normality. The use of distance to estimate dispersal has been discouraged in favor of analyses of movements across a given number of territories (Greenwood and Harvey 1982). However, the territories of Mountain Plovers often overlap with those of neighbors (Graul 1975), and our observations from Montana suggest that individuals have fluid territories that change within (e.g., as a result of nesting phenology or Mountain Plover density) and between years. It is thus extremely difficult, or even impossible, to measure dispersal as the number of territories bypassed before settling.

Model effects.—The fates of nests were determined using several pieces of information, usually a combination of nest age through egg flotation, visual signs of disturbance, the presence of eggshell evidence in collected nest contents (Mabee 1997), and sightings of chicks in or near the nest cup or later (with a banded adult only) on the same prairie dog colony. We considered a nest successful if ≥1 egg hatched.

During each visit to a colony, we visually noted prairie dog activity and signs of possible plague and later assigned plague presence or absence to each nesting attempt. By the end of the Mountain Plover's breeding season, >95% of the prairie dogs within a colony that experienced a plague event succumb to the disease (Collinge et al. 2005, Pauli et al. 2006) and the colony is often hardly recognizable as such (S. J. Dinsmore et al. pers. obs.). A plagued colony showed reduced prairie dog activity, had vegetative growth on burrows, and occasionally had sick or dying prairie dogs present. How the plague moves across the landscape is still not clearly understood, and some colonies experienced more than one such event over the course of our study. Although predation is the largest cause of nest failure in the study area (S. J. Dinsmore et al. pers. obs.), nests also fail as a result of severe weather (high precipitation or extreme temperatures; Dinsmore et al. 2002),

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human disturbance, and abandonment. All nests ($n = 10$) whose fates were directly influenced by human activity were excluded from analysis. We used "year" as a surrogate for annual events such as environmental variables to see whether other effects influenced dispersal.

We developed a set of *a priori* predictions based on previous avian studies to explain Mountain Plover dispersal patterns. In Colorado, male Mountain Plovers defend nest territories that females then choose among (Graul 1973). Thus, we predicted that females would disperse greater distances than males. We predicted, on the basis of the decision-rule theory of the prior-experience hypothesis (Greenwood 1980), that Mountain Plovers that were successful in the previous year would disperse shorter distances than those that were unsuccessful. Plague events also make a colony uninhabitable for a nesting Mountian Plover, and therefore we predicted that birds that nested on colonies that experienced plague in the previous year would disperse greater distances than those that nested on unaffected colonies.

Statistical analyses.—To examine differences in natal dispersal by sex, we used the Wilcoxon rank-sum test in the JMP statistical package, version 7 (SAS Institute, Cary, North Carolina). The effects of plague and year could not be rigorously tested because of small sample sizes. We used the MIXED procedure in SAS, version 9.1 (SAS Institute), to compare breeding dispersal distances within years while accounting for multiple contributions from individuals. During the 14-year period, three individuals contributed two pairs of nesting attempts to the within-year analysis. In the analysis of breeding dispersal distance, we constructed a single mixed model with individual birds as a random effect and the fixed effect of sex of the tending adult. In addition to the distances that Mountain Plovers moved between nesting attempts, we also were interested in the fidelity of birds to their nesting colonies. We modeled colony fidelity as a binary response variable (yes–no) vs. the fixed effect of sex, with individual birds included as random effects, using the GLIMMIX procedure in SAS.

We again used the MIXED procedure in SAS to model between-year breeding dispersal distances. For this analysis, 31 birds contributed two pairs of nesting attempts, three contributed three pairs, and two contributed four pairs. We modeled distances in relation to sex, success or failure of the individual's nest during the previous year, whether or not the colony on which the first nest was located had experienced plague between successive nesting attempts, and a categorical fixed year effect. We also included the two-way interaction of sex and plague because a plot of the dispersal distances suggested that males and females may have responded differently to plague. A plague outbreak is rarely an isolated event and often affects several colonies in proximity to one another. An outbreak is predicted to cause Mountain Plovers, especially males, to disperse farther than normal (Graul 1973). We modeled colony fidelity for between-year movements using the same method as for within-year movements but also included fixed effects of previous nest fate, plague, year, and the two-way interaction of sex and plague. Marginal effects of factors in all models were examined using *F* tests.

To determine whether nest fate (hatching success or failure) in a given year was related to the distance moved from the previous year's nesting attempt, we performed a logistic regression using the LOGISTIC procedure in SAS. The consequences of breeding dispersal are poorly known (Greenwood and Harvey 1982), and results of previous studies have shown that subsequent success of some species has improved as the distance of dispersal increased (Pärt and Gustafsson 1989) whereas that of others showed no improvement (Pasinelli et al. 2007). Again, we included in the model the additive effects of sex of the tending adult, whether the previous nest had been successful or failed, and whether or not the initial nesting colony experienced a sylvatic plague event, along with the two-way interaction of sex and plague. However, we did not include the effects of year because of limited sample sizes. We used all-subsets model selection on the covariates to determine which model was best supported and then added distance to the selected model. We used $\alpha = 0.05$ as the level of statistical significance for all hypothesis tests. Results are presented as means ± SE.

Results

Over the 14-year period, a total of 38 Mountain Plovers (16 males and 22 females among >750 total) banded as chicks returned to nest the following year. The median natal dispersal distance of 10.6 km (mean = 13.0 ± 3.33 km) and 7.9 km (mean = 10.2 ± 1.94 km) for males and females, respectively, did not differ (Wilcoxon-rank sum, $z = 0.40$, df = 36, $P = 0.69$). Two males and two females nested on their natal colony.

Of the individuals that renested within a year after a nest failure ($n = 48$), the 22 males had a median breeding-dispersal distance of 0.3 km (mean = 2.8 ± 1.27 km), whereas the 26 females dispersed a median distance of 0.6 km (mean = 3.0 ± 0.90 km). The difference between the sexes in within-year dispersal distances was not significant (Type III test for fixed effects [MIXED]: $F = 1.87$, df = 1 and 43, $P = 0.27$). Nearly 70% of males and 60% of females renested on the same prairie dog colony, and these rates of colony fidelity did not differ (Type III test for fixed effects [GLIMMIX]: $F = 1.95$, df = 1 and 43, $P = 0.26$).

A total of 159 Mountain Plovers contributed 202 pairs of nesting attempts for analyses of breeding dispersal between years (Fig. 2). We found no significant difference in the dispersal distances of males and females (Type III test for fixed effects [MIXED]: $F = 1.15$, df = 1 and 157, $P = 0.29$) or between individuals that had nested in the previous year on colonies that had or had not experienced a sylvatic plague event ($F = 1.23$, df = 1 and 157, $P = 0.28$). There was also no difference in dispersal distances among years ($F = 1.15$, df = 11 and 157, $P = 0.36$), and the two-way interaction of sex and plague was not significant ($F = 0.58$, df = 1 and 157, $P = 0.45$). However, birds whose nests had been successful the previous year dispersed shorter distances (median = 0.3 km, mean = 3.0 ± 0.55 km; $n = 149$) than birds whose nests had been unsuccessful (median = 0.7 km, mean = 4.6 ± 1.18 km; $n = 53$) ($F = 8.02$, df = 1 and 157, $P = 0.01$).

After controlling for other factors, the proportion of males (66%) and females (50%) that returned to the previous year's colony to nest did not differ (Type III test for fixed effects [GLIMMIX]: $F = 3.52$, df = 1 and 157, $P = 0.07$). If the colony had experienced plague during the previous nesting attempt, ~50% nested on a different colony the following year, and if there had been no plague, about 40% moved to a different colony. This difference, although not significant, was suggestive of a plague effect ($F = 3.82$, df = 1 and 157, $P = 0.06$). However, 66% of birds whose nests had been successful the previous

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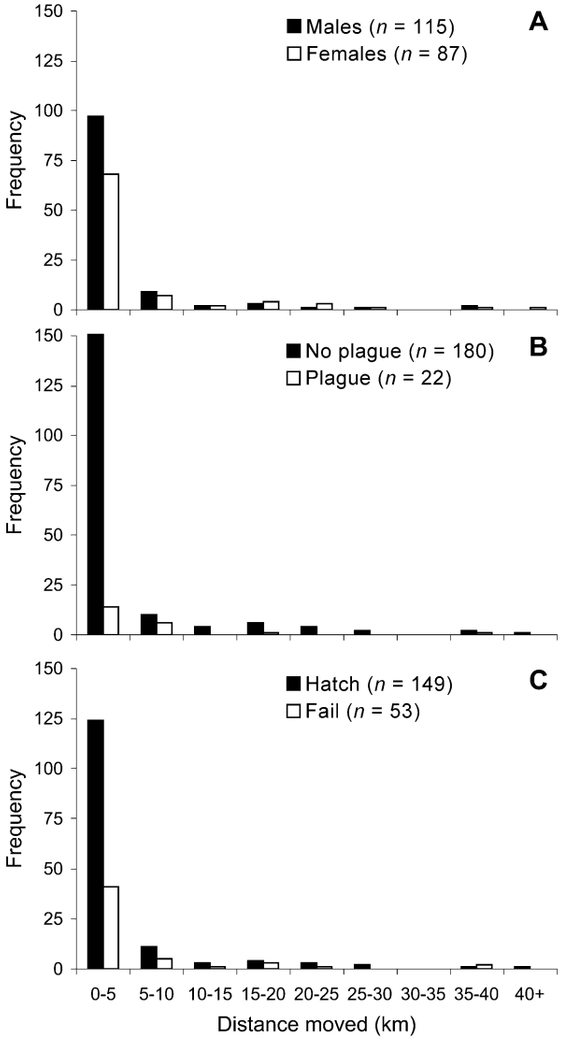

FIG. 2. Number of Mountain Plovers that dispersed different linear distances (km) between pairs of nesting attempts in sequential years in relation to (A) sex of the tending adult (males: median = 0.3, mean = 2.7 ± 0.60 [SE]; females: median = 0.7, mean = 4.3 ± 0.87), (B) presence–absence of sylvatic plague (no plague: median = 0.4, mean = 3.3 ± 0.53; plague: median = 0.9, mean = 4.6 ± 1.84), and (C) previous nest fate (successfully hatched: median = 0.3, mean = 3.0 ± 0.55; failed to hatch: median = 0.7, mean = 4.6 ± 1.18) in southern Phillips County, Montana, 1995–2008.

year returned to the colony on which they had nested previously, but only 40% of birds from nests that had failed returned, and this difference was significant ($F = 4.60$, df = 1 and 157, $P = 0.04$).

The full model containing previous nest fate, sex of the tending adult, presence of sylvatic plague, and the interaction of sex and plague was selected as the best model for predicting subsequent nest fate. However, after the additive effect of ln(distance moved) was included in the model, none of the effects was useful in predicting subsequent nest fate (all $P > 0.05$) and there was large variation within each parameter estimate.

DISCUSSION

Charadriiforms do not appear to respond in a uniform way to nest failure, because some species disperse greater distances after failure (Oring and Lank 1982, Gratto et al. 1985, Flynn et al. 1999) whereas nest fate has no influence on site fidelity or dispersal in other species (Haig and Oring 1988a, b; Wiens and Cuthbert 1988; Colwell et al. 2007). Mountain Plovers behaved like the former, in that dispersal distances were shorter for birds that had bred successfully in the previous year than for those that had failed. The increase in dispersal distance associated with nest failure provides support for the decision-rule theory of the prior-experience hypothesis (Haas 1998), because individuals that were successful tended to be more site-faithful. Previous nest fate was an important influence on dispersal decisions, but the distance that a bird moved was not associated with subsequent nest success, even when further information such as prior nesting success was known. However, other studies of shorebirds have also found no correlation between site fidelity and subsequent nesting success (Oring et al. 1983, Schamel and Tracy 1991).

Dispersal distance of Mountain Plovers was also independent of sex at any stage (natal, within year, and between years). However, because the individual roles of each sex are so similar after eggs are laid, perhaps this should not be unexpected. Sexual differences in the roles that parents assume tend to be associated with differences in dispersal behavior (Clarke et al. 1997). A recent study of Snowy Plover (*C. alexandrinus*), a species with biparental incubation in which males tend to be in charge of brood rearing, found evidence of greater female natal dispersal (Stenzel et al. 2007). However, another study of this same species found no sex differences in dispersal (Colwell et al. 2007), although the former was more rigorous in terms of length of study and sample sizes. Other studies of plovers with biparental care and a male resource-defense system found female dispersal (Clarke et al. 1997) as well as no sex differences (Semipalmated Plover [*C. semipalmatus*]; Flynn et al. 1999). Studies of other Charadriiformes in monogamous, male-territorial systems (sandpipers, gulls, curlews, and godwits) found both greater natal dispersal of females (Clarke et al. 1997) and no influence of sex on dispersal (Semipalmated Sandpiper [*Calidris pusilla*]; Gratto 1988). In the male nest-tending polyandrous Red-necked Phalarope (*Phalaropus lobatus*; Schamel and Tracy 1991) and Spotted Sandpiper (*Actitis macularius*; Reed and Oring 1993), there was evidence of greater natal dispersal by males.

Only 38 of the >750 juvenile Mountain Plovers that we banded in the study area over the 14-year period were known to have nested in their first year. One possible explanation for this low return rate is that juveniles banded as young chicks (<1 week old) may not have survived. Estimates of juvenile annual survival are low (0.06; Dinsmore 2008), and survival is lowest right after hatch but increases as the chicks age (Lukacs et al. 2004, Dinsmore and Knopf 2005, Dinsmore 2008). Thus, many young chicks banded in their first week would not have survived to fledge. Some individuals returned to the study area and were resighted but not found on nests during their first year, whereas other juveniles may have dispersed to nest in other areas, such as Fort Belknap Indian Reservation and southern Valley County. Both are <50 km from our study site, and juveniles color-banded in Phillips County have bred at each site in small numbers (S. J. Dinsmore et al. pers. obs.). The combination of

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these two phenomena could explain why such a small proportion (<5%) returned to the natal area to nest in their first year.

Few studies of within-year breeding dispersal exist, but such movements appear to be more constrained than between-year movements, possibly because the availability of territories is limited (Greenwood and Harvey 1982). This may be especially true for Mountain Plovers in Phillips County, Montana, because prairie dog colonies represent <1% of the landscape. The available habitat is likely to be saturated, which possibly explains the Mountain Plovers' moderate level of sociality and tendency to form loose semicolonies (Graul 1975). At the height of the breeding season, birds that experienced nest failure may be forced to disperse farther because preferred nesting locations may already be occupied. Indeed, within-year movements of >20 km among colonies (P. D. B. Skrade et al. pers. obs.) have been documented. Colwell et al. (2007) found that Snowy Plovers often bred multiple times within a year at a single site rather than move among sites and that males tended to be slightly more sedentary than females. However, this species can produce multiple successful clutches within a breeding season, which is likely to influence dispersal behavior. Mountain Plovers in Montana never produce more than one successful clutch within a breeding season (S. J. Dinsmore et al. pers. obs.), so the time constraints of moving to a new territory and finding another mate may also limit renesting opportunities.

Habitat quality has also been shown to influence avian breeding dispersal (Bollinger and Gavin 1989). In this system, the removal of prairie dogs by sylvatic plague effectively reduces the suitability of a colony for nesting (Augustine et al. 2008). However, the effects of plague on breeding dispersal of Mountain Plovers are not as simple as we hypothesized initially. Half of all the birds that nested on a colony that experienced a plague event attempted to nest on that colony the following year. If a bird initiates its nest early enough in the breeding season, it could potentially be successful on that colony before vegetative growth causes the habitat to become unsuitable by midsummer. Older birds arrive earlier in the breeding season than younger birds (Oring and Lank 1982, Thompson and Hale 1991), and although the ages of Mountain Plovers included in the present study are unknown, those nesting on plagued colonies may be more experienced birds.

We confirmed that previous nesting success is important in predicting the dispersal behavior of Mountain Plovers, but in the future it would be beneficial to further explore the added effects of age and mate fidelity. Both have been found to affect dispersal in other species. Older individuals might be influenced to remain at a site by cumulative successful experiences across multiple years (Greenwood and Harvey 1982), whereas the presence of a previous mate may override the urge to disperse following a failure (Naves et al. 2006). These factors will be challenging to measure in the Mountain Plover because it is difficult to follow known-age individuals through successive nesting attempts and their rapid multiclutch mating system requires genetic analysis of offspring to accurately determine parentage.

Our study, which documented the movements of Mountain Plovers over a large area, is relevant to other species that also breed in highly fragmented habitat that is scattered across a landscape. The decline in Mountain Plovers during the past 40 years has been partially attributed to habitat loss, and information about breeding locations and site fidelity is important for the conservation of this species. The disappearance of the American Bison, increased fire suppression, and removal of prairie dogs from much of the landscape are some of the factors that caused a decrease in suitable nesting habitat (Knopf and Wunder 2006). Domestic cattle have now replaced bison as the predominant grazers, and their effects on vegetation differ. Bison create bare areas and shorter vegetation that is more suitable for Mountain Plovers (Knopf and Samson 1997) because bison typically eat grass closer to the ground than cattle (Hartnett et al. 1997). The decline in prairie dogs in this area through human removal and sylvatic plague (Collinge et al. 2005) has further fragmented breeding sites. Plovers are now possibly forced to disperse greater distances between suitable sites than they did historically. As a result, habitat fragmentation has increased for the Mountain Plover, although we found that they are still able to locate suitable nest sites within several kilometers of familiar territories. To preserve and enhance Mountain Plover breeding habitat, we argue that complexes of prairie dog colonies in proximity to each other should be maintained. Nonetheless, we acknowledge that further study is needed to clarify the role of sylvatic plague on the patterns of fidelity and dispersal in Mountain Plovers in anthropogenically altered landscapes.

Acknowledgments

We are grateful to Iowa State University, the U.S. Bureau of Land Management (Phillips Resource Area, Montana), and Montana Fish, Wildlife, and Parks for financial support. The staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. J. J. Grensten assisted with multiple aspects of the study. Field assistance was provided by A. Brees, T. M. Childers, D. C. Ely, T. Hanks, J. G. Jorgensen, C. McQueary, R. Schmitz, T. Vosburgh, and C. T. Wilcox. We thank B. Matovitch, D. Robinson, and J. Robinson for allowing us access to their lands, and the F. and D. Veseth families for additional support. We also thank P. M. Dixon and A. D. Peterson for statistical advice. The manuscript benefited from careful reviews by V. J. Dreitz, R. R. Koford, C. M. Vleck, N. Warnock, and M. B. Wunder.

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Associate Editor: C. M. Handel

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