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Authors: Hunt, Kelsi L., Dinan, Lauren R., Friedrich, Meryl J., Brown, Mary Bomberger, Jorgensen, Joel G., et al.

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Density Dependent Double Brooding in Piping Plovers (*Charadrius melodus*) in the Northern Great Plains, USA

KELSI L. HUNT[1,*], LAUREN R. DINAN[2], MERYL J. FRIEDRICH[1], MARY BOMBERGER BROWN[3], JOEL G. JORGENSEN[2], DANIEL H. CATLIN[1] AND JAMES D. FRASER[1]

[1]Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061, USA

[2]Nongame Bird Program, Nebraska Game and Parks Commission, Lincoln, Nebraska, 68503, USA

[3]School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska, 68583, USA

[*]Corresponding author; E-mail: hunt0382@vt.edu

Abstract.—Piping Plovers (*Charadrius melodus*) are primarily monogamous birds that usually raise only one brood per season, but rare instances of double brooding have been documented. Piping Plovers breeding in the northern Great Plains, USA were studied in two locations: the Missouri River near the Gavins Point Dam (2005-2013) and the lower Platte River (2008-2013). There were 25 confirmed instances of double brooding on the Missouri River across the 9-year duration of the study. There were no instances of double brooding observed locally on the lower Platte River. However, in 2013, two female Piping Plovers successfully hatched eggs and fledged chicks from nests on the lower Platte River and later were observed nesting for a second time on the Missouri River. Factors predicted to increase the frequency of double brooding are: early nest initiation, male biased sex ratio, age of breeding adults, and decreased nesting density. Our results indicate density is an important factor that accounts for some of the difference in the proportion of double brooding on the Missouri River compared to the lower Platte River. It is likely a combination of factors is responsible for this behavior, previously thought to be rare, in Piping Plovers.

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Key words.—*Charadrius melodus*, density dependence, double brooding, Great Plains, Missouri River, Piping Plover, Platte River.

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Piping Plovers (*Charadrius melodus*) are generally thought to raise one brood per nesting season (Elliott-Smith and Haig 2004). However, a few instances of double brooding have been documented (Bottitta *et al.* 1997; Amirault *et al.* 2004; Elliott-Smith and Haig 2004). Double brooding is defined as successfully hatching eggs and fledging chicks from one nest and subsequently initiating egg laying in a second nest (Yuan 1993). Piping Plovers commonly re-nest if a clutch or young brood (chicks < 5 days of age) is lost, but raising two broods to fledging in a single breeding season is rare (Haig and Oring 1988). A number of factors may affect when and why double brooding occurs in species that typically only raise one brood per breeding season; these include timing of nesting, skewed sex ratios, age of breeding adults, and habitat and food availability (Nagy and Holmes 2005).

The first documented report of double brooding in Piping Plovers occurred at Griswold Point in Old Lyme, Connecticut, in 1989 when a pair of Piping Plovers successfully fledged two chicks from their first nest and later fledged three chicks from a second nest (Bottitta *et al.* 1997). Bottitta *et al.* (1997) documented eight Piping Plover pairs successfully raising two broods during a single nesting season in Connecticut, Maryland, and Virginia along the Atlantic Coast from 1989-1994. The cases of double brooding documented by Bottitta *et al.* (1997) were all thought to involve the same adults parenting the first and second nest, but this was not confirmed in every case. The evidence used to determine these cases

of double brooding involved banded birds (three instances), chicks from the first nest observed in the second nest exclosure while an adult was incubating eggs (one instance), and adult plumage characteristics and proximity of the two nest sites (four instances) (Bottitta *et al.* 1997).

Piping Plovers commonly re-nest with the same mate following nest failure (Haig and Oring 1988), but changing mates during double brooding has been documented (Amirault *et al.* 2004; Elliott-Smith and Haig 2004). The first documented report of polygamous behavior associated with double brooding in Piping Plovers occurred in the Atlantic Coast population in Nova Scotia in 2000 (Amirault *et al.* 2004). It is unknown how regularly polygamy or double brooding occurs in Piping Plovers, but both behaviors seem to be relatively uncommon (Elliott-Smith and Haig 2004).

Although Piping Plovers rarely exhibit double brooding, other species of shorebirds display this behavior more commonly. Killdeer (*C. vociferous*) occasionally double brood with eggs for a second nest being laid before the first brood has fledged (Lenington 1980). In the Gulf of Thailand, Malaysian Plover (*C. peronii*) pairs were reported to double brood, generally laying a successive clutch prior to the first chicks fledging (Yasu*é* and Dearden 2008). In southwestern Sweden, Ringed Plover (*C. hiaticula*) pairs attempted to double brood with the same mate after fledging chicks from their first brood, although this was infrequent due to low fledging success of initial broods (Wallander and Andersson 2003). Mountain Plovers (*C. montanus*) are monogamous with a rapid multiple-clutch mating system where the female lays two clutches and a single adult tends each nest (Graul 1973; Dinsmore 2003). Snowy Plovers (*C. nivosus*) in parts of California are polyandrous double brooders; the female deserts the first brood prior to fledging to locate a new mate and initiate a second nest and, in some cases, males nested for a second time with a new mate after fledging its first brood (Warriner *et al.* 1986). Pacific Dunlin (*Calidris alpina pacifica*) females nesting on the Yukon-Kuskokwim Delta have been observed deserting their initial brood to produce a second clutch with a new mate (Jamieson 2011). Spotted Sandpipers (*Actitis macularius*) are known polyandrous multiple brooders, with females laying several clutches of eggs that are incubated by different males (Emlen and Oring 1977).

Early nest initiation, or an elongated breeding season, has been linked to an increase in double brooding in other shorebird species including Dunlin (*C. a. schinzii*; Soikkeli 1967), Ringed Plover (Wallander and Andersson 2003), Malaysian Plover (Yasué and Dearden 2008), and Pacific Dunlin (Jamieson 2011). A male-biased sex ratio may facilitate double brooding (Soikkeli 1967; Warriner *et al.* 1986) in some shorebird species. Anecdotal evidence from fieldwork on the Missouri River indicated that double brooding may be associated with an increase in first year males as well as decreased nesting density (D. Catlin, pers. commun.). Increased nesting density has also been shown to lead to an increased need for biparental care in Kentish Plovers (*C. alexandrinus*), perhaps due to decreased food availability and increased agonistic interactions between broods (Rittinghaus 1975), which may decrease the occurrence of double brooding.

Prior to this study, double brooding had not been documented in the northern Great Plains population of Piping Plovers. Our objectives were to quantify and examine the occurrence of Piping Plover double brooding in two areas of the northern Great Plains, the Missouri River and the lower Platte River, and to identify factors associated with this behavior. We hypothesized that double brooding would be negatively related to nest initiation date and nesting density as well as related to the age of the breeding birds and a male-biased sex ratio.

METHODS

Study Area

Missouri River. We studied Piping Plovers nesting on sandbars located in the Missouri River, USA on the Gavins Point Reach (42° 51′ N, 97° 29′ W) and Lewis and Clark Lake (42° 51′ N, 97° 47′ W) from 2005-2013 (Fig. 1).

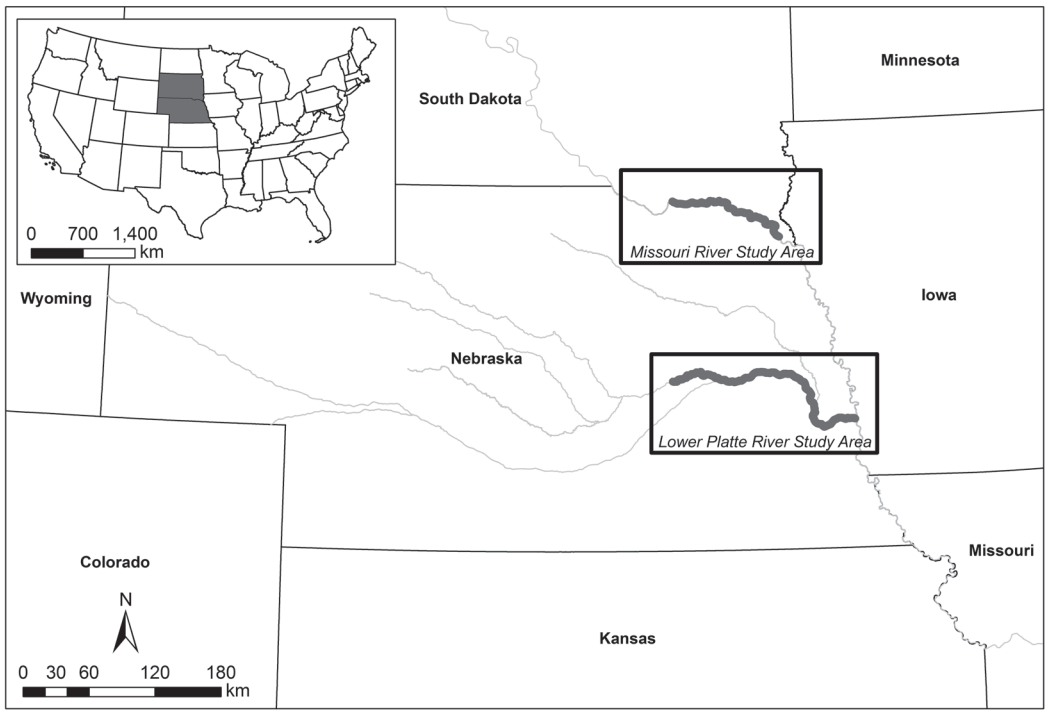

Figure 1. Map of the lower Platte River and Missouri River study areas.

The Gavins Point Reach is unchannelized and extends 95 km downstream from the Gavins Point Dam, which impounds Lewis and Clark Lake. From 2005-2010, the U.S. Army Corps of Engineers built sandbars in the Missouri River to provide nesting habitat for Piping Plovers and Interior Least Terns (*Sternula antillarum athalassos*). In 2011, unusually deep mountain snow and high spring precipitation resulted in high water on the Missouri River that created an abundance of sandbar habitat in 2012 and 2013. Sandbar nesting habitat generally consisted of mudflats and sandflats that were unvegetated or sparsely vegetated with cottonwood (*Populus* spp.) and willow (*Salix* spp.) saplings.

Lower Platte River. We studied Piping Plovers nesting along the lower Platte River in eastern Nebraska from 2008-2013 (Fig. 1). The study area includes midstream river sandbars located in the river and off-river sand and gravel mines and lakeshore housing developments adjacent to the lower Platte River and a small portion of the Loup River. The lower Platte River extends from the Loup-Platte River confluence (41° 23′ 53″ N, 97° 19′ 6″ W) 165 km downstream to where it joins the Missouri River (41° 3′ 12″ N, 95° 52′ 46″ W). The lower Platte River is a relatively dynamic river that continues to create sandbar habitat naturally (Jorgensen *et al.* 2012). The off-river sites typically include a pit lake surrounded by large expanses of bare or sparsely vegetated sand. Most Piping Plovers along the lower Platte River nest at off-river sites because river sandbars suitable for nesting are rarely available at the onset of the nesting season.

Field Methods

Missouri River. During the 2005-2013 nesting seasons (April-July), we searched sandbars for nests by walking transects through all known nesting habitat (unvegetated and sparsely vegetated, wet and dry sand habitat) and by watching Piping Plover behavior. We recorded nest locations using a handheld Trimble GPS unit. We attempted to visit nests every 2-3 days until either failure or hatching was confirmed. There was no nest monitoring in 2010 and reduced monitoring in 2012.

We captured incubating adults using a drop-door trap placed over the nest. Each adult was sexed by plumage (Gratto-Trevor *et al.* 2010) and banded with a unique color combination. We associated an adult with a nest if we captured the bird on a specific nest or if we were able to read its color band combination and subsequently observe it incubating eggs or brooding chicks. We searched for banded adults during all sandbar activities throughout the study. We captured chicks by hand and banded them with a unique color combination. We attempted to resight or recapture chicks every 2-3 days from the time of banding until they were ≥ 25 days old. We continued to resight chicks after fledging until they departed on migration.

Lower Platte River. During the 2008-2013 nesting seasons (April-July), we searched off-river sites and river sandbars for nests by walking transects through nesting habitat (unvegetated and sparsely vegetated, wet and dry sand habitat) and by watching Piping Plover behavior (Brown *et al.* 2013). River conditions varied from year to year, which influenced our ability to monitor

river sandbars, but generally, sandbars were accessed via kayak and searched by foot from early June to early August. We attempted to visit nests at off-river sites every 5-7 days until either failure or hatching was confirmed. We recorded nest locations using a handheld Garmin Oregon 550t GPS unit.

We banded adult Piping Plovers at off-river sites only; we did not band any Piping Plovers on river sandbars. We captured incubating adults using a drop-door trap placed over the nest, and we captured chicks by hand. All birds captured were banded with a unique color combination. We associated an adult or chick with a nest if it was captured on a specific nest or if we were able to read its band combination and subsequently observe it at a nest or with brooding chicks/adults. We searched for banded adults and chicks throughout the study.

Analysis

We defined a double brooding attempt as at least one member of a pair raising a brood to ≥ 15 days while at least one member of the pair initiated a second nest. We excluded re-nests that may have occurred following the loss of young (< 5 days old) chicks. Although 15 days is younger than the typical fledging age (25 days), daily survival between 15-25 days is relatively high and resighting/recapture is relatively low (Catlin *et al.* 2013). We considered a nest successful if we observed at least one egg hatch. Data from 2010 on the Missouri River were excluded due to infrequent nest and brood visits.

We calculated nest initiation dates using the number of eggs and egg floating data (Hays and LeCroy 1972) from our initial nest visit. We used the Welch two sample *t*-test to test for differences in nest initiation dates between double brooding birds and single brooding birds. After excluding nests known to be associated with double brooding, we randomly chose the same number of single brood nests in each year for comparison. For Piping Plovers of unknown age (i.e., banded as adults), we calculated minimum possible age using year at initial banding as age one. We tested for differences in age between a double brooding Piping Plover and its first or second mate using the Welch two sample *t*-test. To calculate the yearly proportion of double brooding attempts, we divided the number of double brooding nests by the total number nests monitored in a given year.

We did not have total habitat amounts for all years and locations throughout the study, so we calculated 'average group size' by dividing the total number of nests in a given year by the number of breeding sites (sandbars and off-river sites) used by nesting Piping Plovers in that year, and used this as an index of nest density. To investigate whether average group size was a reliable index of nest density, we conducted a Pearson correlation analysis between nest density and average group size on the Missouri River from 2005-2013. We used a multiple linear regression to examine the effect of average group size and the difference between sites on the occurrence of double brooding. All analyses were completed using statistical program R (R Development Core Team 2014), and statistical significance was set at < 0.05. Means are reported as ± SE unless otherwise indicated.

RESULTS

There were no recorded instances of double brooding occurring locally on the lower Platte River from 2008-2013 from our sample of 384 monitored nests. However, in 2013 two female Piping Plovers that successfully fledged ≥ 1 chick on the lower Platte River were later reported nesting for a second time on the Missouri River. These two instances have been included in the following analyses of double brooding on the Missouri River. The correlation ($r = 0.87$, $t_6 = 4.38$, $P = 0.005$) between nest density and average group size on the Missouri River from 2005-2013 indicated that average group size was a reliable index of nest density.

We monitored 1,824 nests on the Missouri River from 2005-2013 (excluding 2010), and the proportion of double brooding attempts varied across years (Fig. 2). From 2005-2013, there were 25 instances of Piping Plovers successfully producing at least one 15-day-old chick and initiating a second nest. There were no instances of double brooding in 2006 or 2011, and the highest number ($n = 7$, 3.9%) occurred in 2012. In three cases, a pair remained together for the second nest, but in all other instances a different mate was involved in the second nest (28 individuals total).

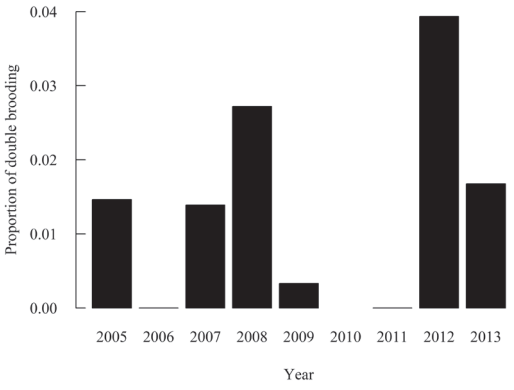

Figure 2. The proportion of double brooding attempts to total number of nests initiated by Piping Plovers on the Missouri River (2005-2013). Data were not available for 2010.

Mean nest initiation date varied on the lower Platte and Missouri Rivers between years, with the lower Platte River initiation dates being slightly earlier on average (Table 1). Nest initiation dates for the first nest of double brooding Piping Plovers was significantly different than initiation dates for randomly selected nests of single brooding Piping Plovers (two-tailed $t_{39.4} = -5.22$, $n = 28$, $P < 0.001$). The mean time between initiation dates of first and second nests of double brooders was 43 ± 2.7 days, and the mean time between hatching of the first nest and initiation of the second nest was 10 ± 2.8 days.

Of the 25 instances we observed, 80% ($n = 20$) of the double brooding birds were female, 8% ($n = 2$) of the double brooding birds were male, and 12% ($n = 3$) involved both the male and female of a pair double brooding. Double brooding Piping Plovers were of similar mean age (2.4 ± 0.3 years) to their first mate (2.0 years; two-tailed $t_{52.6} = 0.87$, $n = 28$, $P = 0.39$); however, the age of double brooders was significantly different than their second mate (1.4 years; two-tailed $t_{42.3} = 2.68$, $n = 28$, $P = 0.01$). In all instances, when mate switching occurred between the first and second nests, the second mate was not known to have nested previously in that year. Average group size varied from 2.1-15.5 pairs per nesting site (Fig. 3). Average group sizes on the Missouri River (8.4 ± 1.6 pairs per nesting site) were more variable than those on the lower Platte River (3.1 ± 0.3 pairs per nesting site) (Fig. 3). Average group size and study area (Missouri River vs. lower Platte River) accounted for 66% of the variation of the proportion of double brooding (*Adj.* $R^2 = 0.66$, $F_{2,10} = 12.6$, $P = 0.002$). The proportion of double brooding was lower on the lower Platte River than the Missouri ($\beta = -0.027 \pm 0.005$, $P < 0.001$) and as average group size (i.e., nest density) increased, the proportion of double brooding decreased ($\beta = -0.002 \pm 0.0006$, $P < 0.001$; Fig. 4).

Nest success for the second nest in a double brooding attempt was 64.0% ($n = 16$) and of those nests, 31.3% ($n = 5$) reared at least one chick to ≥ 15 days of age. The mean number of chicks fledged per double brooder was 1.26 ± 0.19, and in one instance a female fledged a total of eight chicks (2012). Twenty-four (85.7%) of the total individuals that double brooded were resighted the year following their double brooding attempt.

DISCUSSION

Piping Plovers have previously been described as serially monogamous breeders (Elliott-Smith and Haig 2004). This study is one of the first to report double brooding being observed relatively consistently in a population of Piping Plovers. In 2013, two Piping Plovers were observed successfully nesting on both the lower Platte and Missouri Rivers in a single breeding season. This represents only the third confirmed instance of long-distance transit (> 100 km) double brooding in Piping Plovers. Two occurrences of long-distance double brooding were documented in the Great Lakes population,

Table 1. Double brooding and nest initiation dates on the Missouri River and the lower Platte River from 2005-2013. 'n/a' indicates that data were not available and '—' indicates that double brooding did not occur.

Year	Proportion of Double Brooding	Missouri River Mean Nest Initiation (all nests)	Missouri River Mean Nest Initiation (double brooding)	Lower Platte River Mean Nest Initiation (all nests)
2005	0.015	28 May	9 May	n/a
2006	0.000	23 May	—	n/a
2007	0.014	21 May	9 May	n/a
2008	0.027	29 May	15 May	22 May
2009	0.003	28 May	22 May	30 May
2010	n/a	n/a	n/a	19 May
2011	0.000	4 June	—	25 May
2012	0.039	21 May	4 May	19 May
2013	0.017	31 May	6 May	28 May

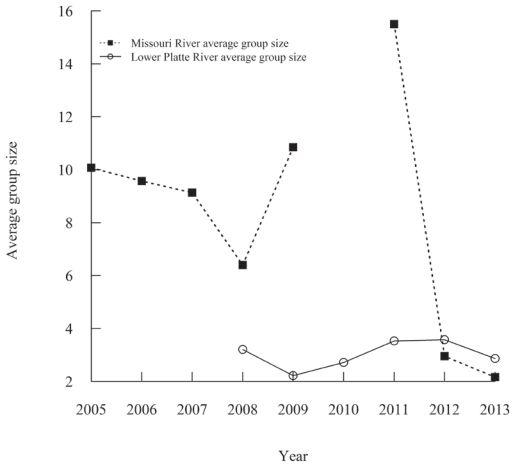

Figure 3. Average group size of Piping Plovers (an index for density) on the Missouri River from 2005-2013 and on the lower Platte River from 2008-2013. Data were not available for 2010 for the Missouri River.

in which the same female Piping Plover successfully fledged chicks at one location then dispersed approximately 100 km south in 2010 and 142 km south in 2012 and double brooded with a different mate (S. Saunders, pers. commun.).

Similar to other Charadriiformes, female Piping Plovers in our study were more likely to double brood than males, deserting their initial brood prior to fledging to initiate another nest. Female Snowy Plovers breeding in coastal California are known to desert their brood prior to fledging to initiate a second nest, leaving the male to attend to the initial brood (Warriner *et al.* 1986). Jamieson (2011) reported that of seven Pacific Dunlin in the Yukon-Kuskokwim Delta, Alaska, that attempted to double brood, 86% were females that left the initial brood 2.6 days (on average) after hatching to locate another mate.

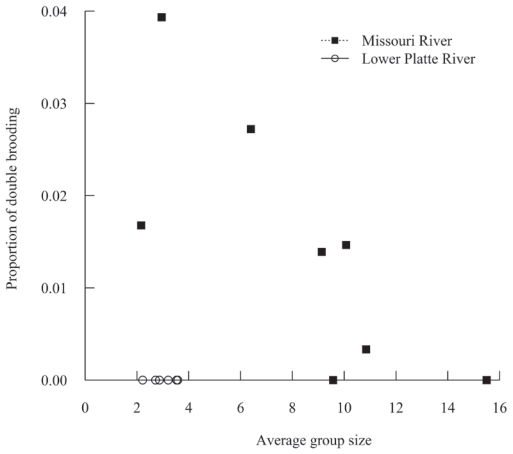

Figure 4. The proportion of double brooding as it related to average group size (an index for density) on the Missouri River from 2005-2013 and on the lower Platte River from 2008-2013. Data from 2010 were not available.

Given that double brooding was previously considered rare in Piping Plovers, there are several factors that may explain why this behavior occurred more frequently on the Missouri River than on the lower Platte River or in other parts of the Piping Plover's breeding range. One factor is nest initiation date. In all years of our study, Piping Plovers involved in double brooding initiated their first nest before the average initiation date for all nests (Table 1). The earlier a nest is initiated, the more time a Piping Plover has to hatch the first nest successfully, locate a mate, and initiate a second nest. Early nest initiation or an elongated breeding season has been linked to an increase in double brooding in other shorebird species (Dunlin: Soikkeli 1967; Ringed Plover: Wallander and Andersson 2003; Malaysian Plover: Yasué and Dearden 2008; Pacific Dunlin: Jamieson 2011). Our results indicate that nest initiation dates of double brooding Piping Plovers differed from randomly selected nests initiated by single brooding Piping Plovers. However, mean nest initiation dates on the lower Platte River were slightly earlier than on the Missouri River throughout the study, suggesting that double brooding is the choice of individual birds and therefore an individual effect and not a population effect.

The second and third factors explaining higher rates of double brooding on the Missouri River may be a male biased sex ratio and the age of the breeding birds. Other research has indicated skewed sex ratios are associated with double brooding in Snowy Plovers (Warriner *et al.* 1986) and Dunlin (Soikkeli 1967). The majority of Piping Plovers involved in double brooding in our study were females that initiated second nests with males significantly younger than themselves.

It may be the case that these younger males, who are less experienced breeders, either migrated and arrived later at nesting sites and consequently were unable to acquire mates, or were unable to compete with older males to secure mates when their arrival was synchronous. Thus, their only local reproductive option was to wait for a double brooding female. In the Great Lakes population of Piping Plovers, a male-biased sex ratio can be attributed, in part, to males having higher pre-fledging survival than females (Saunders and Cuthbert 2015). From our work on the Missouri River, we know that females have a higher probability of dispersal (Friedrich *et al.* 2015), and increased dispersal and movement may lead to lower survival in Piping Plovers (D. Catlin, unpubl. data), which may contribute to a sex ratio biased toward males. Sex data for Piping Plovers nesting on the lower Platte River is unavailable; therefore, we are unable to compare the sex ratios between the two areas. A skewed sex ratio is a plausible reason why there were more frequent observations of double brooding on the Missouri River compared to the lower Platte River or other parts of the Piping Plover's breeding range.

The fourth factor is 'average group size,' which we used as an index of nesting density. Our results indicated that average group size was a significant factor accounting for the variation in the proportion of double brooding. On the Missouri River, the years with the highest proportion of double brooding (2008 and 2012) were also two of the years with the smallest average group sizes. In 2008, habitat built on Lewis and Clark Lake coupled with low water releases from the Gavins Point Dam resulted in increased nesting habitat. A flood during the 2011 breeding season created an abundance of new sandbar habitat in 2012. Density could be associated with a male biased sex ratio because inexperienced breeders (1-year-old birds) arrive on the breeding grounds approximately 28 days after experienced breeders (2+ year-olds; Catlin *et al.* 2015), and with sufficient nesting habitat available, they are able to establish territories for themselves. When densities are high, inexperienced breeders arriving later are unable to secure a territory and their site fidelity decreases (Catlin *et al.* 2015), potentially leading to a decrease in the probability of double brooding.

Average group size on the Missouri River fluctuated, sometimes substantially, between years, reflecting a variable amount of habitat available to nesting Piping Plovers. In contrast, average group size on the lower Platte River remained relatively constant over the duration of the study. This suggests nesting sites on the lower Platte River may be at or near carrying capacity. Given productivity on the lower Platte River (0.61-1.44 chicks/pair; M. Bomberger Brown, unpubl. data.), it is expected that average group size should increase in some years if the population is below carrying capacity. However, increased average group size or density has not been observed in the lower Platte River. If nesting sites on the lower Platte River are fully occupied, young males may be unable to claim territories, lowering the opportunity for double brooding. In recent years on the lower Platte River, 78.1% (n = 300) of Piping Plover nesting has occurred at off-river sites, where the amount of available nesting habitat is relatively stable from year-to-year compared to river sandbars (M. Bomberger Brown, unpubl. data.). Average group size was smaller on the lower Platte River during the 2009 breeding season. An unusually large amount of sandbar nesting habitat was available in 2009 as a result of a high flow event in 2008 and relatively low flows during the 2009 nesting season (Brown and Jorgensen 2009).

Our data show lower Platte River Piping Plovers are capable of long-distance double brooding, with their second nests occurring on the Missouri River when average group sizes are low (2012 and 2013), again suggesting that density may be a limiting factor in the occurrence of double brooding. The Gavins Point Reach of the Missouri River is one of the last relatively free-flowing portions of the Missouri River. Although water levels are controlled by the Gavins Point Dam, there are opportunities for the creation of new habitat (e.g., low water levels or sand accretion caused by flooding) that may facili-

tate double brooding. In many portions of the Piping Plover breeding range, creation of nesting habitat (e.g., by barrier island over-washing) is often followed by coastal protection measures (e.g., dune building) that quickly reduce habitat. The infrequency of sustained habitat creation may be another reason that double brooding is rare in such places.

Increased nesting density has been shown to lead to an increased need for biparental care in Kentish Plovers, perhaps due to decreased food availability and increased agonistic interactions between broods (Rittinghaus 1975). On the Missouri River, both intraspecific aggression and interspecific aggression with Interior Least Terns occur when nesting densities are high (Catlin 2009). The need for biparental care to protect pre-fledged broods may be another reason why double brooding of Piping Plovers on the Missouri River decreased in years when average group sizes were highest.

The results of this study suggest that density is an important factor in the occurrence of Piping Plover double brooding depending on the nesting site, and that the combination of early nest initiation by individuals, a male biased sex ratio, and the age of breeding birds may also contribute. This is the first study to confirm multiple occurrences of double brooding using individually identifiable (color banded) Piping Plovers, and it highlights the ability of Piping Plovers to make long-distance transits for double brooding. Our data suggest that double brooding behavior in Piping Plovers may be more common than previously thought.

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