



## FEMALE SITE FAMILIARITY INCREASES FLEDGING SUCCESS IN PIPING PLOVERS (*CHARADRIUS MELODUS*)

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**ABSTRACT.**—Reproductive success commonly improves with age in birds. However, it is difficult to determine whether this phenomenon is due to breeding experience or other age-related factors because most potential explanatory factors are positively correlated. Using a 17-year database, we investigated how age, breeding experience, location experience, and pair-bond experience influenced Piping Plover (*Charadrius melodus*) reproductive success in the Great Lakes region. Reproductive success was measured as number of offspring fledged per pair for 415 successful nests during 1993–2009. We controlled for individual and site variation with random effects and tested for increased reproductive success associated with age, prior breeding experience, prior location experience, and prior pair-bond experience using generalized linear mixed models. Reproductive success increased with location-specific breeding experience of females and declined when females moved to a new location. After statistically controlling for these effects, we found no additional effect of male age, male experience, or pair experience. Additionally, fledging success declined with later hatching dates, so we examined the relative influence of age and experience on hatch date and determined that older females and males bred earlier. Our results indicate that improvement in reproductive success with age in Piping Plovers has two components: a direct effect of female location experience on fledging success, and an indirect effect of timing of breeding, which leads to greater reproductive success through earlier nesting by older males and females. Actions by resource managers to promote breeding philopatry and successful early nesting attempts may enhance reproductive success of this federally endangered population. Received 6 June 2011, accepted 27 February 2012.

Key words: age-related reproduction, *Charadrius melodus*, fledging success, location experience, Piping Plover, timing of breeding.

### La Familiaridad de las Hembras con el Sitio Incrementa el Éxito de Emplumamiento en *Charadrius melodus*

**RESUMEN.**—El éxito reproductivo comúnmente mejora con la edad en las aves. Sin embargo, es difícil determinar si este fenómeno se debe a la experiencia reproductiva o a otros factores relacionados con la edad, porque muchos de los posibles factores explicativos están positivamente correlacionados entre sí. Usando una base de datos de 17 años, investigamos cómo la edad, la experiencia reproductiva, la experiencia con la ubicación y la experiencia con el vínculo de pareja influyen en el éxito reproductivo de *Charadrius melodus* en la región de los Grandes Lagos. El éxito reproductivo fue medido como el número de crías emplumadas por pareja con base en 415 nidos exitosos entre 1993 y 2009. Controlamos por la variación individual y del sitio con efectos al azar, y probamos si el incremento en el éxito reproductivo se asociaba con la edad la experiencia reproductiva anterior, la experiencia con la ubicación anterior, y la experiencia con el vínculo de pareja anterior usando modelos lineales generalizados mixtos. El éxito reproductivo aumentó con la experiencia de las hembras con una ubicación específica y disminuyó cuando las hembras se mudaron a una nueva localidad. Después de controlar por estos efectos, no encontramos un efecto adicional de la edad del macho, la experiencia del macho ni la experiencia con el vínculo de pareja. Además, el éxito de emplumamiento disminuyó con las fechas tardías de eclosión, por lo que examinamos la influencia relativa de la edad y la experiencia en la fecha de eclosión, y determinamos que las hembras y los machos más viejos se reproducen más temprano. Nuestros resultados indican que la mejora en el éxito reproductivo con la edad en *C. melodus* tiene dos componentes: un efecto directo de la experiencia de las hembras con la ubicación sobre el éxito de emplumamiento, y un efecto indirecto del momento en que sucede la reproducción, que lleva a un mayor éxito reproductivo por medio de la anidación más temprana de hembras y machos más viejos. Las acciones tomadas por los administradores de recursos para promover la filopatría reproductiva y los intentos exitosos de anidación temprana pueden promover el éxito reproductivo de esta población federalmente amenazada.

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ORGANISMS THAT REPRODUCE repeatedly throughout their lifetimes often have age-specific patterns of reproductive success (Forslund and Pärt 1995). In birds, reproductive performance typically improves with age in younger age classes, often followed by a senescent decline in older individuals (Nur 1984, Forslund and Pärt 1995, Fowler 1995, Newton and Rothery 2002). Four general hypotheses have been raised to explain increased reproductive performance with age among younger age classes. The selection and recruitment hypotheses address population-level changes that occur as a result of selective mortality or recruitment of individuals at the population level, whereas the breeding experience and restraint hypotheses propose improvements in reproductive performance that can occur within individuals.

The selection hypothesis (Curio 1983) proposes that the positive relationship between age and reproductive success occurs through the selective loss of poor breeders (Forslund and Pärt 1995, Mauck et al. 2004, Steenhof and Heath 2009), whereas the recruitment hypothesis predicts that increased reproductive performance is due to later recruitment of high-quality breeders (Forslund and Pärt 1995, Martin 1995, Steenhof and Heath 2009). Both of these hypotheses are attributable to variation among individuals and depend on positive correlations in life-history traits among individuals: fecundity with survival in the case of the selection hypothesis and fecundity with age at first breeding for the recruitment hypothesis (Mauck et al. 2004).

In addition to age-related improvements within cohorts, two categories of hypotheses address age-related improvements that occur within individuals: (1) age-related improvements in competence (i.e., amelioration of constraints or improvement of breeding experience) and (2) age-related changes in allocation of reproductive effort (i.e., restraints; Curio 1983, Forslund and Pärt 1995, Martin 1995, Steenhof and Heath 2009). The breeding experience hypothesis posits that the effects of previous breeding experience may improve later breeding performance, either because of more efficient physiological processes or fine tuning of behaviors closely associated with reproduction (Pärt 1995). Thus, previous experience in activities such as laying and incubating eggs, brooding offspring, or tending young may lead to increased reproductive performance by older birds if such behaviors can be learned and therefore improve with accumulated experience (Pyle et al. 1991). Shared breeding experience of pairs is an important component of this hypothesis because it enables individuals to gain knowledge about how to effectively coordinate incubation and brood-rearing duties with previous mates (Haig and Oring 1988, Mauck et al. 2004). Potential improvements are not limited to breeding experience, however; older birds may be more productive because of improvements in behaviors not directly associated with reproduction, such as feeding skills, intraspecific competition, or predator avoidance (Nol and Smith 1987, Wooller et al. 1990, Weimerskirch 1992, Brown and Roth 2009). Such age-related improvements seem most likely to explain the evolution of deferred breeding, particularly in birds with complex foraging behaviors (Burger 1980, Marchetti and Price 1989). For young birds, reproductive effort likely accentuates patterns caused by constraints; as birds gain experience and become more likely to succeed in reproduction, their allocation of effort to reproduction should also increase (Forslund and Pärt 1995, Mauck et al. 2004).

As an individual's experience increases, the return per unit effort increases; thus, effort should increase with age and experience (Mauck et al. 2004). But as individuals approach senescence and survival or reproductive abilities decline, the restraint hypothesis also predicts that older individuals should invest more heavily in current reproduction because they have declining reproductive value (Forslund and Pärt 1995, Brown and Roth 2009, Steenhof and Heath 2009).

In addition to these direct potential influences on fledging success, age and experience can indirectly enhance reproductive performance through their influence on arrival and breeding times (Roche et al. 2008, Brudney 2009). Older, more experienced birds typically nest earlier in the breeding season (Oring and Lank 1982, Hatch and Westneat 2007, García-Navas and Sanz 2011) and are likely to have the greatest amount of prior breeding experience and site familiarity. Because reproductive performance typically declines seasonally in birds (Rohwer 1992, Brinkhof et al. 2002), earlier breeding can lead to further increases in reproductive success for older and more experienced birds.

Despite numerous investigations, the degree to which age, individual experience, and their interactions affect variation in timing of breeding and fledging success remains unclear (Nol and Smith 1987, Pyle et al. 1991, Martin 1995, Pärt 1995, Mauck et al. 2004). The rarity of large samples of marked individuals of both known age and known experience, further confounded by strong correlations between age and breeding experience, have made it difficult to determine whether improvements in reproductive performance are caused by breeding experience or other age-related factors (Brown and Roth 2009). Our study uses 17 years of data (1993–2009) on Piping Plovers (*Charadrius melodus*) breeding in the Great Lakes region of North America to explore causes of age-related variation in timing of breeding and fledging success. The Great Lakes Piping Plover population is almost completely marked and monitored, with >90% of nesting adults and >95% of offspring individually banded (Roche et al. 2008), and annual detection probabilities of breeding birds approaching 100% (LeDee et al. 2010), which allows the development of detailed reproductive histories for most individuals in the population. Although age, breeding experience, nest location experience, and pair-bond experience tend to be positively correlated, their effects are not indivisible because Piping Plovers begin breeding at different ages and have varying degrees of mate and site fidelity (Haig and Oring 1988, Roche et al. 2008, Gratto-Trevor et al. 2010). Here, we exploit this variability in individual histories to determine which of the following four factors have the greatest influence on timing of breeding and fledging success: (1) physiological or behavioral maturation, which represents improvements due to age per se, regardless of prior breeding experience; (2) prior breeding experience, which may allow for the development of individual breeding skills, such as incubation and rearing of offspring; (3) prior site experience, which may provide local knowledge, such as safe nesting sites or improved foraging sites; and (4) prior mate experience, which may aid in the coordination of incubation and brood-rearing duties among pair members. By using random effects models to assess among-individual variation in these parameters, we also address the potential for selective mortality or deferred recruitment to produce these patterns.

**METHODS**

*Focal species and study area.*—The Piping Plover is a small shorebird endemic to North America and restricted to three breeding populations: Atlantic Coast, Great Plains, and Great Lakes (Haig et al. 2005). The Great Lakes population of Piping Plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan, Superior, and Huron (U.S. Fish and Wildlife Service [USFWS] 2003); most of the population occurs in Michigan. Listed as federally endangered in 1986 (USFWS 1985), the Great Lakes population has numbered from 17 to 71 known breeding pairs (F. J. Cuthbert and S. P. Saunders unpubl. data). Females typically produce a 4-egg clutch, offspring are precocial, and both parents assist in rearing young. Females, however, are more prone to abandon the brood prior to fledging (Cairns 1982). Nests are covered with wire exclosures to reduce egg predation as soon as they are discovered (Melvin et al. 1992), and recreational activities are managed to reduce human disturbance in nesting and brood-rearing areas (USFWS 2003). Our study used data from known nesting locations between 1993 and 2009 (Fig. 1).

*Field data collection.*—Since 1993, surveys for breeding pairs of Piping Plovers have been conducted at the beginning of each breeding season at historical, recent, and potential nesting habitats. Most breeding pairs were monitored every 1 to 4 days from nest initiation until the nest was destroyed or abandoned or until young disappeared or fledged. Data collected during monitoring included identity of Piping Plover pairs (based on unique color bands; Wemmer et al. 2001) and number of eggs or offspring present at each visit. Approximately 98% of individuals were of known age, and the remaining 2% were assigned minimum ages of 1 the first time they were recorded breeding.

*Data summary and analyses.*—We defined fledging success as the number of offspring per brood that survived to fledging age (~23 days old; Brudney 2009), based on pairs that hatched at least one

young. We used fledging success for pairs that hatched at least one egg because nearly all nests were protected by predator exclosures during our study period (100% of nests were exclosed from 2004–2009), as mandated under our Federal Endangered Species Permit. Thus, hatching success was not a reliable measure of reproductive performance, because it primarily reflected how quickly and effectively nests were found and fenced by investigators, rather than varying levels of parental investment. Nests where fledging count was not recorded were excluded from analyses, as were nesting attempts where the identity and experience of at least one pair member was unknown ( $n = 415$ , representing 71% of all nests monitored during our study period). We defined a pair as a male and female Piping Plover that mated, produced eggs, and shared incubation of a nest ( $n = 320$  unique pairs comprised of 181 females and 183 males).

Previous studies have demonstrated substantial spatial variation in survival of plover young (Colwell et al. 2007, Le Fer et al. 2008, Brudney 2009), and we wished to control for this source of variation in our analyses. We defined a breeding location as a single, continuous stretch of appropriate nesting and brood-rearing habitat (mean  $\pm$  SD = 3.33  $\pm$  2.89 km;  $n = 20$ ) separated from other sites by >1.5 km of inhospitable shoreline (Fig. 1; Wemmer et al. 2001, Haffner et al. 2009). Our measures of location experience utilized these same definitions and refer to an individual’s or pair’s familiarity with one of these 20 breeding locations, but not necessarily to a specific nesting territory or home range (Haffner et al. 2009). Because locations differed from each other in terms of offspring survival (Brudney 2009), we added location to our statistical models as an *a priori* random effect (Zuur et al. 2009). Similarly, we added male and female identity as second and third random effects to account for pseudoreplication of individuals (Zuur et al. 2009) and to test for among-individual variation in reproductive performance as posited by the selection and recruitment hypotheses (van de Pol and Verhulst 2006).

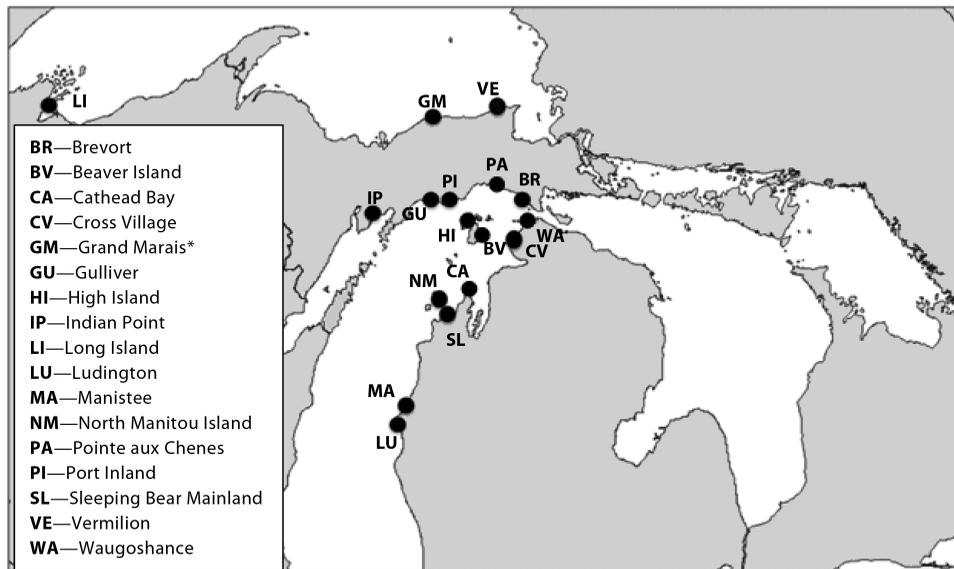


FIG. 1. Distribution of Great Lakes Piping Plover nest-site locations during 1993–2009. Asterisk indicates that the Cross Village (CV) location also includes Bliss and Sturgeon Bay, which are within 1.6 km of each other.

We initially used two different methods to tally breeding and location experience. The first method was based on all nesting attempts, including renests, and allowed breeding experience to accumulate within a single breeding season. By this measure, individual experience was the sum of all known nesting attempts that an individual had made in its lifetime, location experience was the sum of all nesting attempts at a particular breeding location, and pair experience was the sum of all nesting attempts that these two Piping Plovers had made together. Hence, a pair of yearling Piping Plovers that nested together for the first time and had two failed nesting attempts at location A prior to hatching their third nest at location B would receive values of 1 each for age, 3 for individual and pair breeding experience, and 1 for location experience when evaluating their third nesting attempt. The second method tallied only annual breeding experience, where (1) breeding experience increased only if a given individual or pair nested in a previous year and (2) location experience increased only if a given individual or pair nested at the same location in a previous year (in the above example, all measures would be coded as 1). We found that the annually based covariates were better predictors of fledging success than their within-season complements in all cases, and we therefore based all measures of breeding and location experience on the second method, which tallied only annual breeding experience. We also tallied instances when individuals either changed breeding locations or changed mates between years to directly assess the effects of moving to a new breeding location or breeding with a new partner.

We used generalized linear mixed models (package lme4) in R, version 2.12.0 (Bates and Sarkar 2006), to investigate sources of variation in hatch date (HDATE, where 1 = 1 June; modeled using a normal distribution) and fledging success

(FLEDGE, range: 0–4 fledged young per brood; modeled using a Poisson distribution). For each response variable (HDATE or FLEDGE), we considered 12 potential covariates: (1) female age (AGEF), (2) female breeding experience (EXPF), (3) female location experience (LEXPf), (4) female mate change (FMACH = 1 if new mate, 0 if previous mate), (5) female location change (FLOCH = 1 if new location, 0 if previous location), (6) male age (AGEM), (7) male breeding experience (EXPM), (8) male location experience (LEXPm), (9) male mate change (MMACH), (10) male location change (MLOCH), (11) pair breeding experience (EXPP), and (12) pair location experience (LEXPP; Table 1).

Because individual covariates were highly correlated with each other, we used a forward selection approach to model-fitting to minimize problems with autocorrelation. For both the hatch-date and fledge analyses, we began with a null model that included an intercept, random location effect, and random individual effects for both males and females. To this model we added each of the 12 covariates individually and ranked these models on the basis of Akaike's information criterion corrected for small sample size ( $AIC_c$ ). After each step, we discarded any uninformative covariates that led to increased  $AIC_c$  scores (Arnold 2010). If multiple covariates yielded a reduction in  $AIC_c$  compared to the null model, the model with lowest  $AIC_c$  was used as a base model for considering additional undiscarded covariates. If the linear term for a given covariate was selected, we also considered the quadratic term (e.g., age<sup>2</sup>); if two or more covariates were selected, we also evaluated interaction terms. When additional covariates no longer led to a reduction in  $AIC_c$ , the best-supported model from the previous step was retained as the top supported model. Means are reported  $\pm$  SD unless otherwise indicated.

TABLE 1. Variables used to estimate hatch date and fledging success of Great Lakes Piping Plover pairs during 1993–2009. Variables are organized according to the type of experience that each describes: age, prior site experience, prior breeding experience, and prior mate experience. The quadratic form of these variables (e.g., AGEF<sup>2</sup>) was also included in the models. Fledging success (FLEDGE) and hatch date (HDATE) were the response variables. Nest-site location (LOCATION) and individual identity (IDF and IDM) were included as random effects in all models.

| Experience       | Variable                  | Definition   |
|------------------|---------------------------|--|
|                  | FLEDGE                    | Fledging success; the number of chicks per brood that survived to fledging age |
|                  | HDATE                     | Hatch date of first egg in clutch (1 = 1 June)                                 |
|                  | LOCATION                  | Nest-site location   |
|                  | IDF                       | Unique female identification number  |
|                  | IDM                       | Unique male identification number  |
| Age-related      | AGEF, AGEF <sup>2</sup>   | Age of female within a pair  |
|                  | AGEM, AGEM <sup>2</sup>   | Age of male within a pair  |
| Site-related     | LEXPm, LEXPM <sup>2</sup> | Male's location experience, measured annually                                  |
|                  | LEXPf, LEXPF <sup>2</sup> | Female's location experience, measured annually                                |
|                  | FLOCH                     | Nesting location change by female  |
|                  | MLOCH                     | Nesting location change by male  |
| Breeding-related | EXPM, EXPM <sup>2</sup>   | Number of years male has nested  |
|                  | EXPF, EXPF <sup>2</sup>   | Number of years female has nested  |
| Mate-related     | EXPP, EXPP <sup>2</sup>   | Number of years a given pair has nested together                               |
|                  | LEXPP, LEXPP <sup>2</sup> | Pair's location experience, measured annually                                  |
|                  | FMACH                     | Mate change by female  |
|                  | MMACH                     | Mate change by male  |

RESULTS

The mean hatch date was 20 June ± 13 days (90% range: 25 May–16 July), and the mean number of young fledged per brood was 2.0 ± 1.42 offspring (variance = 2.02). Although the variance was identical to the mean, fledging success was not distributed as a perfect Poisson variable ( $\chi^2 = 114.0$ ,  $df = 4$ ,  $P < 0.0001$ ) because of excessive numbers of Piping Plover nests that fledged zero or 4 offspring. On average, males initiated nesting at an older age than females (males: 1.54 ± 0.75 years,  $n = 149$ ; females: 1.32 ± 0.60 years,  $n = 146$ ;  $t = 2.90$ ,  $df = 293$ ,  $P = 0.004$ ), and males also bred for more years than females (Table 2). Sample sizes were adequate ( $n = 10$  to 180) for individual-based measures of age and experience out to 5–7 years and for pairs out to 3 years. Location-specific sample sizes ranged from a low of 1 nest at High Island to 73 nests at Sleeping Bear Dunes.

Fledging success declined with hatch date (regression equation: FLEDGE = 0.92 [SE = 0.07] – 0.012 [SE = 0.003] \* HDATE;  $n = 415$ ). The best-supported model for hatch date included linear and quadratic terms for both female and male ages. As Piping Plovers aged, both females and males nested earlier in the season; however, the effect was stronger among females and diminished among older age classes (Fig. 2). After accounting for female and male ages, no other covariates were related to hatch date. The best-supported model for fledging success included female location experience, female location change, and their interaction (FLEDGE = 0.56 [SE = 0.08] + 0.07 [SE = 0.03] \* LEXPF + 0.11 [SE = 0.22] \* FLOCH – 0.24 [SE = 0.14] \* LEXPF \* FLOCH; Table 3). Fledging success increased with accumulated location experience of the breeding female and suffered a substantial setback when females moved to a new location (Fig. 3).

Random location effects indicated that fledging success was greater, on average, at Sleeping Bear Dunes and lower at Cross Village (Fig. 4A), whereas hatching dates were earlier at Sleeping Bear Dunes and later at Vermilion (Fig. 4B). Individual random effects were strongly supported for hatch date ( $\sigma_{\text{FEMALE}} = 12.35 \pm 3.51$ ;  $\sigma_{\text{MALE}} = 5.91 \pm 2.40$ ), but not for fledging success (both estimates were zero).

DISCUSSION

Previous studies have documented seasonal declines in reproductive success for Piping Plovers in the Great Plains and Atlantic populations (Knetter et al. 2002, Harris et al. 2005, Cohen et al. 2009), similar to what we found for Great Lakes Piping Plovers. Such declines are widespread in birds (Daan et al. 1988, Rohwer 1992, Brinkhof et al. 2002) and are often driven by seasonal declines in clutch size (Daan et al. 1988, Hochachka 1990). Although Piping Plovers lay fewer eggs in late-season nesting attempts (Cohen et al. 2009), most clutches contain 4 eggs, regardless of initiation date. For Piping Plovers, greater rates of nest predation and partial or total brood losses are more likely responsible for declining reproductive success in late-nesting pairs (Roche et al. 2008, Brudney 2009, Cohen et al. 2009). Seasonally declining offspring survival may be a result of deteriorating environmental conditions, such as decreases in food abundance (Van der Jeugd et al. 2009), or seasonal changes in abundance or behavior of predators could lead to greater predation risks for late-hatched broods (Kruse et al. 2001). Alternatively, seasonally declining survival might be correlated with differences in parental quality, with older, more experienced adults breeding earlier in the season (García-Navas and Sanz 2011), a pattern that was strongly supported by our data.

We found that timing of breeding was strongly influenced by male and female ages, but not by prior breeding or location experience. These results corroborate conclusions from numerous other studies (Nur 1984, Nol and Smith 1987, Forslund and Pärt 1995), all of which suggest that older birds nest earlier in the breeding season than younger ones. Female age had a stronger effect on hatch date than did male age, with females nesting earlier in the season than males among the oldest age classes. During nearly every breeding season in recent years, numerous (about 8–15) unpaired males and few (about 1–3) unpaired females were observed (F. J. Cuthbert and S. P. Saunders unpubl. data). Thus, older females are not limited by availability of mates and are able to initiate nesting immediately after arrival on the breeding grounds. By contrast, older males must frequently wait for a potential mate and end up breeding with younger and later-nesting females. Although neither male nor female age was an important predictor of

TABLE 2. Number of brood-rearing attempts by Great Lakes Piping Plover pairs from 1993–2009, according to male and female age. Individuals appear multiple times if they nested successfully in >1 year.

| Male age | Female age |     |    |    |    |    |    |   |   |    | Σ  |
|----------|------------|-----|----|----|----|----|----|---|---|----|----|
|          | 1          | 2   | 3  | 4  | 5  | 6  | 7  | 8 | 9 | 10 |    |
| 1        | 47         | 20  | 6  | 9  | 1  | 1  | —  | 1 | 1 | —  | 86 |
| 2        | 30         | 31  | 15 | 7  | 4  | 2  | 3  | — | — | —  | 92 |
| 3        | 13         | 27  | 19 | 8  | 6  | 3  | 2  | 2 | — | —  | 80 |
| 4        | 9          | 14  | 13 | 11 | 8  | —  | —  | — | — | —  | 55 |
| 5        | 4          | 4   | 8  | 6  | 7  | 4  | —  | 1 | — | —  | 34 |
| 6        | —          | 5   | 5  | 6  | 5  | 3  | 2  | — | — | —  | 26 |
| 7        | 1          | 1   | 3  | 2  | 5  | 3  | 2  | 1 | 1 | —  | 19 |
| 8        | 1          | —   | 1  | 3  | —  | 2  | 1  | 1 | — | 1  | 10 |
| 9        | 1          | 1   | —  | —  | —  | —  | —  | 1 | 1 | —  | 4  |
| 10       | —          | —   | 1  | —  | —  | 1  | 1  | — | 1 | —  | 4  |
| 11       | —          | 1   | —  | 2  | —  | 1  | —  | — | — | —  | 4  |
| 12       | —          | —   | 1  | —  | —  | —  | —  | — | — | —  | 1  |
| Σ        | 106        | 104 | 72 | 54 | 36 | 20 | 11 | 7 | 4 | 1  |    |

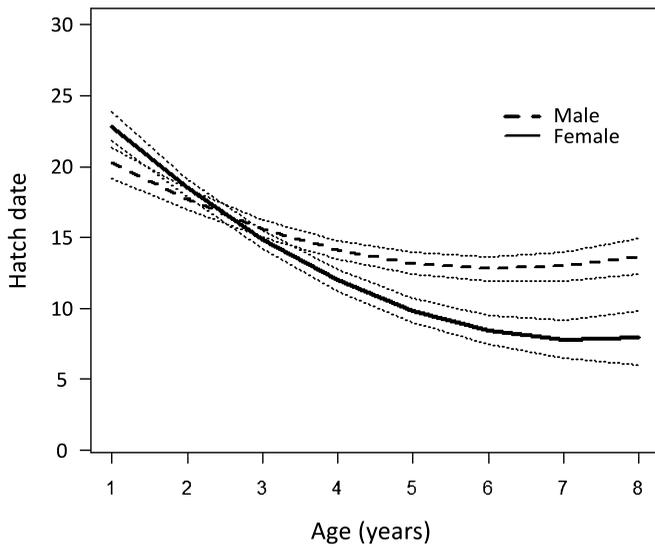


FIG. 2. Effects of female ( $n_f = 181$ ) and male ( $n_m = 183$ ) ages on hatch date (1 = 1 June) during 1993–2009 in the Great Lakes region, excluding renesting attempts. Solid regression line represents the linear model where hatch date was modeled as a function of male and female age, with male age held constant. The dashed regression line represents the model where female age was held constant.  $HDATE = \beta_0 + \beta_1 * age_f + \beta_2 * age_f^2 + \beta_3 * age_m + \beta_4 * age_m^2$ , where  $\beta_0 = 36.5 \pm 1.83$  [SE],  $\beta_1 = -5.12 \pm 0.83$ ,  $\beta_2 = 0.37 \pm 0.09$ ,  $\beta_3 = -2.75 \pm 0.71$ , and  $\beta_4 = 0.21 \pm 0.07$ . Dotted lines indicate  $\pm$  SE.

fledging success, both were important predictors of hatching date, and because earlier-hatched broods were more successful, timing of hatching nevertheless translates into enhanced fledging success for early-season breeders. Several possible mechanisms can explain why age might affect timing of breeding so strongly but have no bearing on fledging success. First, timing of breeding is often dictated by arrival times, and older, more experienced birds frequently arrive earlier than younger birds (Oring and Lank 1982, Nol and Smith 1987, Forslund and Pärt 1995, Potti 1998, Colwell et al. 2010). This may be because younger, more inexperienced birds arrive when the competition from established birds is reduced

(Oring and Lank 1982). Also, older birds may have more foraging experience and, therefore, be in better condition on the wintering grounds, allowing them to migrate and nest earlier (Alisauskas and Ankney 1985, Forslund and Pärt 1995, Morrison et al. 2007).

Female location familiarity was the most important predictor of fledging success, even though site fidelity in Piping Plovers is male-biased (Haig and Oring 1988). In socially monogamous shorebirds, fidelity to a specific nesting location is generally male-biased because males locate and defend territories before females arrive (Johnson et al. 1993, Flynn et al. 1999). In Semipalmated Plovers (*C. semipalmatus*), returning adult males nearly always settled on the same or an adjacent territory in successive breeding seasons, whereas females were able to choose among multiple breeding opportunities and were less likely to return to the nesting territory used in previous years (Flynn et al. 1999). Similarly, female Piping Plovers are more likely to change nesting locations after reproductive failure, whereas males often return to breed on the same territory every year, regardless of previous reproductive failure (Haig and Oring 1988). As in other plovers (Warriner et al. 1986), female Piping Plovers often abandon their broods and depart on fall migration earlier than males (Cairns 1982). As a result, female site fidelity is weaker at both the beginning and the end of the breeding season (Flynn et al. 1999). Because females use more locations than males, there is greater potential for females to learn which locations are best for raising young and to return to these locations in subsequent years (Haig and Oring 1988, Rioux et al. 2011). Hence, females are more likely to acquire location experience at sites where they have had previous success in reproduction. This interpretation was further supported in the present study by the importance of female location change as the second and only other predictor of fledging success. On average, females that moved to a new location experienced a decrease in fledging success from 2.1 to 1.5 chicks.

Familiarity with a nest-site location is considered valuable because it facilitates food exploitation, territory defense, and predator avoidance (Wiens and Cuthbert 1988), but it is not clear why these same benefits would not also accrue to males. Although males also gain site familiarity from reuse of previous sites, their fidelity to potentially poor territories may preclude development of a strong correlation between site familiarity and fledging success (Cohen et al. 2006). In addition, there was no apparent benefit

TABLE 3. Model rankings for top-supported models used to estimate fledging success (FLEDGE) for Great Lakes Piping Plover pairs from 1993–2009. Models were ranked according to differences in Akaike’s information criterion ( $\Delta AIC_c$ ) and Akaike weights ( $w_i$ ). Important covariates for females (F), males (M), and pairs (P) included location experience (location), location change (lchange), and an interaction term (F location\*F lchange). All models included an intercept term as well as location, male identity, and female identity as random effects on the intercept ( $k = 4$  parameters).

| Model   | $\Delta AIC_c^a$ | Deviance | Parameters (n) | $w_i$ |
|---|------------------|----------|----------------|-------|
| F location + F lchange + F location*F lchange | 0.00             | 508.2    | 7              | 0.50  |
| F location + F lchange                        | 1.10             | 511.3    | 6              | 0.29  |
| F location                                    | 3.90             | 516.1    | 5              | 0.07  |
| F lchange                                     | 4.20             | 516.4    | 5              | 0.06  |
| F location + M lchange                        | 4.80             | 515.0    | 6              | 0.05  |
| P location                                    | 6.40             | 518.6    | 5              | 0.02  |
| Null model                                    | 8.60             | 522.8    | 4              | 0.007 |

<sup>a</sup> $AIC_c$  of the top model was 522.2.

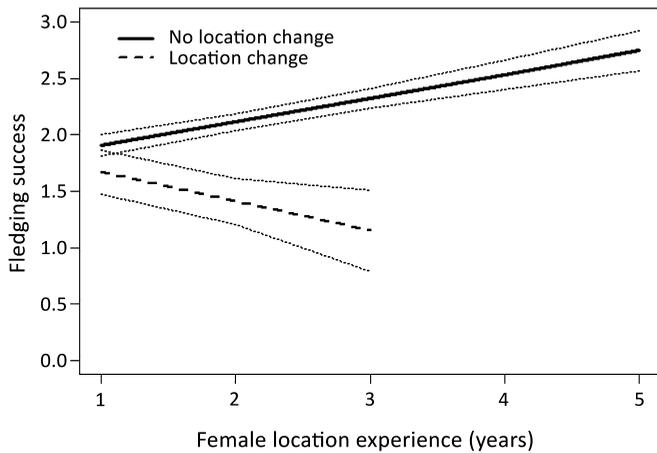


FIG. 3. Effects of female location experience and female location change on fledging success of Piping Plovers in the Great Lakes population. Solid regression line represents fledging success as a function of female location experience and the interaction term, for females that did not change locations (i.e., female location change held constant at FLOCH = 0). The dashed regression line represents fledging success for females that did change locations (i.e., female location change held constant at FLOCH = 1). Dotted lines indicate  $\pm$  SE. Graphs include 95% of the observed range of variation in female location experience.  $FLEDGE = 0.56 \pm [SE = 0.08] + 0.07 [SE = 0.03] * LEXPF + 0.11 [SE = 0.22] * FLOCH - 0.24 [SE = 0.14] * LEXPF * FLOCH$ .

from year-to-year mate retention in our study. Haig and Oring (1988) found that 71% of surviving Piping Plovers returned to their former breeding sites, whereas only 19% repaired with the same mate, although former mates were present. Similarly, Wiens and Cuthbert (1988) demonstrated that 84% of all returning Piping Plovers at Lake of the Woods nested within 200 m of their previous nest site, but only 45% of pairs reunited when both male and female were present the next season.

Our analysis suggests that most improvements in reproduction with age in Piping Plovers occur within individuals, and not at the population level. For fledging success, individual random effects were not significant, indicating no consistent variation among individuals in reproductive performance. Such among-individual variation is essential to the selection and recruitment hypotheses (Mauck et al. 2004). Although hatch date varied among individuals, our analysis showed that hatch date also improved with age within individuals. Finally, our results provide strong evidence that individual experience with a breeding location is the primary driver for increased reproductive success with age in Piping Plovers. This result supports the breeding experience hypothesis, indicating that previous experience, with nesting sites in this case, can improve later reproductive performance. Female familiarity with nest-site locations significantly influenced fledging success, implying that knowledge and behaviors not directly associated with reproduction enhance Piping Plover fledging success. We believe that female experience at a given nest site could account for variation in reproductive success in other widely distributed species of birds as well. Additionally, male and female ages are significant predictors of hatch date, which, in turn, is a significant predictor of fledging success.

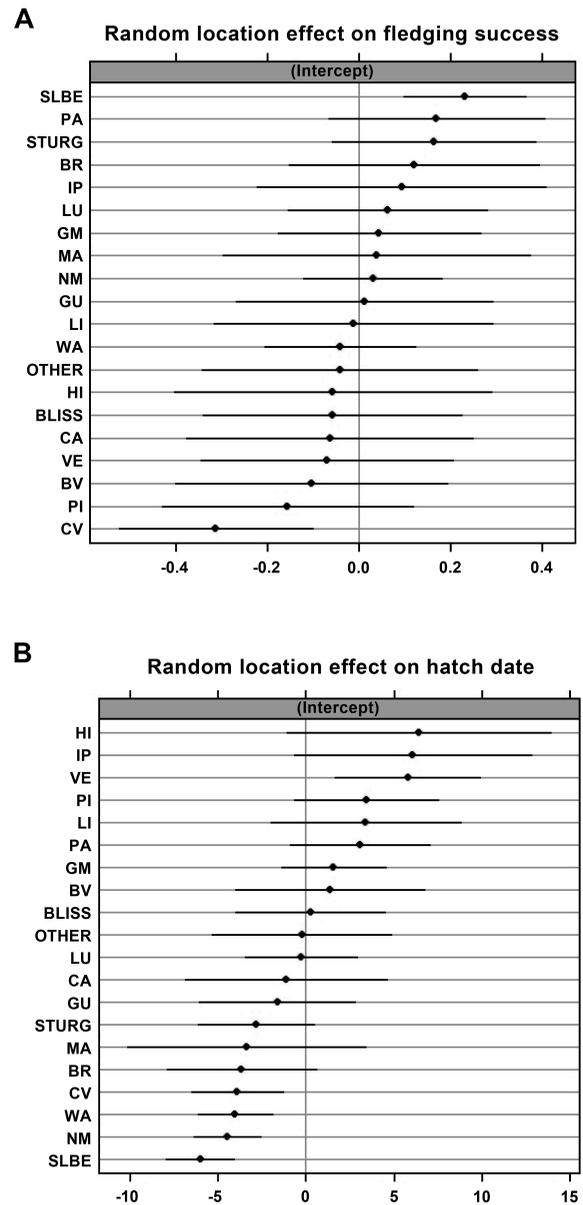


FIG. 4. Prediction intervals of the random location effect on (A) fledging success and (B) hatch date. Breeding sites are listed on the y-axis of both figures, and their influence (either positive or negative) on each response variable is shown along the x-axis. In panel A, all locations overlap zero except for SLBE (Sleeping Bear Dunes, greater success) and CV (Cross Village, lower success). In panel B, all except 5 sites overlap zero; birds at 4 sites, including Sleeping Bear Dunes, nested earlier than average, whereas birds at Vermilion (an Upper Peninsula site) nested later than average. See Figure 1 for nest-site locations and abbreviations (STURG = Sturgeon Bay).

These findings have important conservation implications for management of this endangered population. For example, early-laid nests are likely to fledge more young, and these young are also more likely to survive their first winter (Roche et al. 2008), emphasizing the importance of finding and protecting the earliest nests so that they hatch successfully. Our results also emphasize the importance

of protecting established breeding sites where Piping Plovers can accrue breeding experience over multiple years. Any human disturbance event such as beach grooming, public recreation, and pets off leash (F. J. Cuthbert and S. P. Saunders unpubl. data), as well as anthropogenic flooding of beaches (Gratto-Trevor and Abbott 2011), can prevent Piping Plovers from acquiring location experience that will allow them to maximize their fledging success.

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