Differential Parental Care by Adult Mountain Plovers, *Charadrius montanus*

Stephen J. Dinsmore[1,2] and Fritz L. Knopf[3]

[1]Department of Wildlife and Fisheries, Mississippi State University, Box 9690, Mississippi State, Mississippi 39762 USA
[2]Current address: Department of Natural Resource Ecology and Management, 339 Science II, Iowa State University, Ames, Iowa 50011 USA
[3]U.S. Geological Survey, Fort Collins Science Center, 2150-C Centre Avenue, Fort Collins, Colorado 80526-8118 USA

We studied chick survival of the Mountain Plover (*Charadrius montanus*) in Montana and found that chicks tended by females had higher survival rates than chicks tended by males, and that chick survival generally increased during the nesting season. Differences in chick survival were most pronounced early in the nesting season, and may be related to a larger sample of nests during this period. When compared to information about the nest survival of male- and female-tended plover nests, our chick data suggest a trade-off for adult plovers between the egg and chick phases of reproduction. Because Mountain Plover pairs have clutches at two nests at two different locations and show differential success between the sexes during the egg and chick phases, we offer that the Mountain Plover breeding system favours optimizing annual recruitment in a dynamic ecologic setting driven by annually unpredictable drought, grazing, and predation pressures.

Key Words: Mountain Plover, *Charadrius montanus*, chick survival, Montana

The Mountain Plover (*Charadrius montanus*) is an uncommon and locally distributed breeding bird of the western Great Plains (Knopf 1996). The mating system, described as rapid multi-clutch (Graul 1973), is unusual in birds and involves two clutches per pair per year, each clutch incubated by a single adult (Dinsmore 2001). The female is thought to lay a complete clutch for the male first, and then a second clutch at a different site for herself. The time between the start of incubation for each sex has not been well studied, but was 7-10 days for a small sample of nests in Montana (S. J. Dinsmore, personal observation). Because of this unusual mating system, Mountain Plovers offer an opportunity to investigate breeding strategy differences that may result from the sex of the tending adult. Earlier work with this species has shown differential nest survival by sex of the incubating adult during the incubation stage (Dinsmore et al. 2002); it is not known if these patterns extend through the chick phase to fledging.

Although many aspects of Mountain Plover biology have been well studied, there is little detailed information about the survival of plover chicks. Miller and Knopf (1993) estimated brood survival in northeastern Colorado and calculated a daily chick survival rate of 0.979; the probability that a chick survived the 36-day fledgling period was 0.466. Knopf and Rupert (1996) estimated the daily survival of plover chicks at 10-day age intervals and noted that survival generally increased with the age of the chick. Lukacs et al. (2004) estimated chick survival in east-central Colorado and found that daily survival was lowest immediately after hatch, and quickly increased within 4 days post-hatch. None of those studies addressed whether chick survival

was related to the sex of the tending adult or varied seasonally. Here, we report estimates of daily chick survival of Mountain Plovers in Montana and attempt to understand how survival is influenced by the sex of the tending adult and day within the nesting season.

Methods

Study area

We studied Mountain Plovers in a 3000-km^2 area in southern Phillips County in north-central Montana (47°40'–47°55'N, 107°35'–108°30'W; Figure 1). The study area is bounded by the Missouri River to the south, the Sun Prairie and Content roads to the east, Beaver Creek to the north, and Highway 191 to the west. Approximately 2250 km^2 of the study area is in public ownership with the Bureau of Land Management (BLM, Malta Field Office) and the U. S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge). This area is a mixed-grass prairie with sagebrush (*Artemisia* spp.) flats bordering the southwestern edge of the Prairie Pothole Region (Knowles et al. 1982; Olson and Edge 1985; Dinsmore et al. 2002). All of our work took place on active Black-tailed Prairie-dog (*Cynomys ludovicianus*) colonies that are used preferentially by Mountain Plovers in Montana (Knowles et al. 1982; Knowles and Knowles 1984; Dinsmore 2001).

Capture and marking

During the 1999 nesting season, we fitted 28 nest-tending, adult Mountain Plovers with 3.0 g radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota) to allow us to monitor the survival of chicks within broods. Adult plovers were captured 1-4 days

prior to hatching date with a walk-in trap placed over the nest. On capture, we collected a feather sample from each adult for gender determination (see Dinsmore et al. 2003). Radio transmitters were glued to the mantle feathers of the adult using an epoxy (Titan Corporation, Lynnwood, Washington). Most adult plovers carried the transmitters until their chick(s) fledged and all transmitters were shed when the birds moulted prior to their fall migration. Chicks were marked with a unique series of four UV stable Darvic coloured leg bands (A. C. Hughes, London) and an aluminum U.S. Geological Survey band to allow individual identification. There were no adult or chick mortalities or injuries attributable to capture or handling. The Colorado State University Animal Care and Use Committee approved the field methods used in this study (Protocol 98-134A-01).

Using information from egg floatation (Dinsmore et al. 2002), we knew the exact hatch date for eggs in each nest and typically monitored chick survival at 1-5 day intervals post-hatch. On each brood check, we located the adult bird using a hand-held Yagi antenna and observed the number of chicks and identity of each chick that was present. We ceased to monitor chicks when they fledged at an age of 33-36 days (see Knopf 1996).

Modeling chick survival

We modeled the daily survival of plover chicks using the nest survival model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999). This model is similar to the Kaplan-Meier model that is typically used for telemetry data (Pollock et al. 1989), except that it does not require that the exact failure date be known. In our study, plover broods were not checked daily, so losses of individual chicks could only be assigned to an interval. We used an estimate of 35 days as the fledging date, except in cases where we knew that the fledging date differed (but never by more than 2 days). In a few cases, the tending adult lost its transmitter. In those cases, we censored the data at the last known brood check.

In our analyses, we considered four models to explain variation in chick survival of Mountain Plovers: (1) a model with constant survival [$S(.)$], (2) a model where chick survival differed based on the sex of the tending adult [$S (sex)$], (3) model #2 plus an additive effect of a linear time trend [$S (sex + T)$], and (4) model #2 plus an additive effect of a quadratic time trend [$S (sex + TT)$]. The $S(.)$ model is akin to a Mayfield estimate and implied that chick survival was constant across the entire nesting season, irrespective of date or sex of the tending adult. The $S(sex)$ model implicitly allowed chick survival to differ based on the sex of the tending adult. We were uncertain whether this was an important influence on chick survival, but deemed it a relevant question based on significant differences in the incubation stage (Dinsmore et al. 2002). The $S(sex + T)$ and $S(sex + TT)$ models added seasonal variation in chick survival to the sex difference
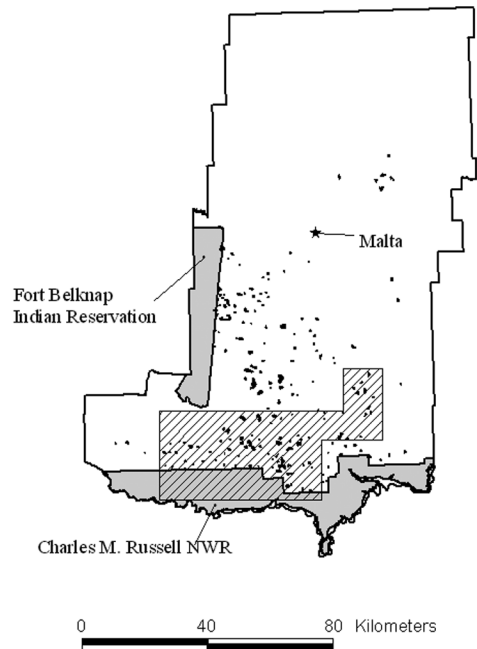

FIGURE 1. Map of Phillips County, Montana showing the distribution in 2000 of Black-tailed Prairie Dog colonies. The stippled regions show an Indian Reservation and National Wildlife Reserve. The hatched portion is the study area.

model. Based on our knowledge of plover biology, we suspected that chick survival might generally increase during the nesting season (Knopf and Rupert 1996), but were unsure whether this pattern might be linear or curvilinear.

We assessed the fit of the nest survival model to our chick survival data using a chi-square test of independence of the fates of chicks within broods as a function of brood size. We computed the expected values for the test statistic as the product of the number of broods in each clutch size (always two or three chicks) and the probability of observing that outcome. The latter probability was calculated as the product of survival (# surviving/total) and mortality (# dying/total) within each possible brood outcome. For example, the probability (Pr) of observing a brood of three chicks where only one survived is 3 * Pr(surviving)* Pr(dying)^2. We estimated over-dispersion as $\hat{c} = \frac{\chi^2}{d.f.}$ and made this adjustment in MARK.

We used the methodology of Burnham and Anderson (2002) to identify the best model(s) and make inferences about the factors influencing chick survival in plovers. We used Akaike's Information Criterion (AIC; Akaike 1973), corrected for possible small sample bias and over-dispersion (QAICc), to rank the set of candidate models. QAIC provides a means of objectively ranking a set of models and then selecting a "best ap-

proximating" model or models for inference (Burnham and Anderson 2002). We used QAICc values to compare the relative distances between the best approximating model and each competing model. Generally, models with QAICc values <2 have strong support while those with QAICc values >10 have little support (Burnham and Anderson 2002). Normalized Akaike weights (w_i) were also computed for each model to provide another measure of the relative importance of each model. Finally, we model averaged parameter estimates across all candidate models to obtain the "best" estimate(s) of chick survival (Burnham and Anderson 2002).

Results

We monitored 27 plover broods comprising 77 chicks (one adult plover died before its eggs hatched) during a 61-day period from 11 June to 10 August 1999. Two plovers (one male and one female) lost their transmitters in late June. Hatch dates varied, although we had slightly more broods early in the nesting season. The sample of tending adults was male-biased (18 males versus 9 females).

The nest survival model fit our chick survival data well ($\chi^2_6 = 7.08$, P = 0.31), and our estimate of overdispersion was $\hat{c} = 1.18$. We found good evidence for an effect of sex on brood survival (Table 1) with chicks in male-tended broods having lower daily survival ($\hat{\beta}_{male}$ = -0.78 on a logit scale, SE = 0.42, 95% CI was −1.60, 0.05). This effect was always negative in the top three models. In addition to the sex effect on chick survival, we found evidence that survival varied during the nesting season (Table 1). The best model (w_i = 0.53) had a quadratic time effect on survival, but a model with a linear effect on survival was nearly as good (QAICc = 0. 29, w_i = 0.46). Chick survival differed the most early in the nesting season, and after that was similar between male- and female-tended chicks. In both models, daily chick survival generally increased during the nesting season (Figures 2 and 3).

Discussion

Our results, while intriguing, should be interpreted with caution. By using information from all chicks within a brood, we risked violating the assumption of independent fates. It is important to note that violation
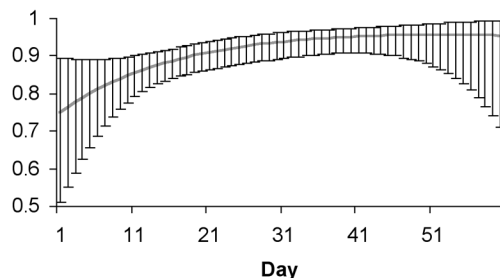

FIGURE 2. Daily survival rates (95% CI) for Mountain Plover chicks tended by a male parent in Montana, 1999. Day 1 corresponds to 11 June.
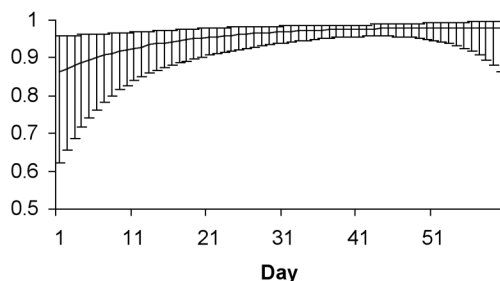

FIGURE 3. Daily survival rates (95% CI) for Mountain Plover chicks tended by a female parent in Montana, 1999. Day 1 corresponds to 11 June.

of the independence assumption does not affect the parameter estimates, but does provide estimates of precision that are too small (Flint et al. 1995). Our test of independence of fates did not reveal any major violation of this assumption, although our sample size of broods was small. However, our observations and previous work with this species had shown that there was severe brood reduction within the first 1-2 weeks post-hatch (personal observation), but that many broods still fledged one or more chicks. Thus, attentiveness by the parent or some other factor was most likely the cause for chick losses, independent of the fates of other chicks in a brood.

Each component of the avian life cycle must be fully understood before inferences can be made regarding

TABLE 1. Summary of model selection results for the chick survival of Mountain Plovers in southern Phillips County, Montana, 1999. Models are ranked by ascending QAICc; w_i is the model weight and K is the number of parameters. Daily chick survival ($\hat{S}_i$) was modeled to include no time effects (.), a linear time trend (T), a quadratic time trend (TT), and the effect of the gender of the tending adult (sex). QDeviance is computed as $-2[\log_e(L(\hat{\theta})) - 2\log_e(L_s(\hat{\theta}))]$ where $\hat{\theta}$ represents a maximum likelihood estimate whose log-likelihood is evaluated for the model in question [$L(\hat{\theta})$] and for the saturated model [$L_s(\hat{\theta})$].

Model	QDeviance	K	QAICc	QAICc	w_i
S (sex + TT)	206.68	4	214.73	0.00	0.53
S (sex + T)	208.99	3	215.02	0.29	0.46
S (sex)	218.10	2	222.12	7.38	0.01
S (.)	234.16	1	236.16	21.43	0.00

population processes. Information from some components (e.g., nest survival) is relatively easy to collect, but for others (e.g., chick and juvenile survival) it is more difficult, especially with precocial species like the Mountain Plover (see Lukacs et al. 2004). Collectively, such detailed information will present a clearer picture of the breeding cycle, and may hint at biological processes that influence success in each stage.

In an earlier study (Dinsmore et al. 2002), we showed that male-tended Mountain Plover nests had much higher survival during the incubation stage than did female-tended nests. We speculate that this results from some combination of temporal variation (male plovers are believed to tend the first nest), differential nest attentiveness, and the different physiological contributions of each sex (e.g., female plovers expend extra energy to produce eggs) early in the nesting cycle. Young Mountain Plovers are precocial (Knopf 1996) and typically leave the nest within hours of hatching, making it difficult to ask questions about possible differences in the survival of chicks in male- and female-tended broods.

Our results indicate that Mountain Plover chicks tended by the female have higher survival than those tended by the male, the opposite of what occurs during the incubation stage. Few birds share the same reproductive strategy as the Mountain Plover, and we were unable to find other published studies that addressed differential chick or brood survival as a result of the sex of the tending parent. A similar reproductive strategy has been well described for some species of North American quail (Burger et al. 1995; Pope and Crawford 2001), although these species differed from the Mountain Plover in adult sex ratio, nest initiation dates, and mean clutch size.

So what does this mean? Male-tended Mountain Plover nests are more successful than female-tended nests, which result in a greater number of broods with a male parent. But during the fledgling stage, female-tended chicks have greater survival, even though there are fewer female-tended broods (Dinsmore et al. 2002). The ultimate cause(s) for this apparent trade-off are unknown, although we can pose two possible explanations. For successful early nests, which tend to be male-tended (Dinsmore et al. 2002), the adult male may still be engaged in courtship activities with later nesting females. This could result in a drop in brood attentiveness, and a resulting decline in the survival of chicks in male-tended broods. The reverse pattern would not be expected for females because a female with a brood may lack the physiological capability to produce an additional clutch.

A second explanation, not necessarily independent of the first, attempts to reconcile the parenting conflicts of male plovers. Despite the asynchrony in nest initiation between the sexes, it appears that both members of the pair forage together during the incubation period (Graul 1973). In this scenario, the male may be in a conflict situation as he enters brood rearing while the female is still incubating. His attempts to maintain the pair bond might initially compromise his attentiveness to newly hatched chicks, resulting in lowered chick survival early in the brood stage. Larger differences in chick survival early in the nesting season may be a result of our larger sample of broods during this, the peak period of brood rearing.

The major evolutionary question that is still unanswered is, "What are the relative contributions of each sex to annual recruitment?" On the basis of this and other studies of the Mountain Plover, we conclude that male and female plovers attain similar rates of productivity with male plovers having higher nest survival and lower chick survival and female plovers showing a reverse pattern. These opposite patterns likely favor sustained productivity in the climatically unpredictable drought cycles of the Northern Great Plains. Putting the clutch of six eggs in two different nests at two different sites, each raised by a different adult, speaks to the flexibility in this breeding system that may have evolved in a highly unpredictable ecological landscape subject to major drought cycles, intensive grazing, and fluctuating predator populations.

Acknowledgments

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