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Parental behaviour of a precocial species: implications for juvenile survival

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Summary

1. Parents determine habitat selection for precocial young by leading their young to foraging areas until the chicks attain full independence. There are potential benefits and costs to reproductive success associated with changing habitats while caring for young. This study investigated the relationship between different types of habitats and their quality on chick survival and brood movements of a declining upland shorebird, the mountain plover *Charadrius montanus*.

2. From 2004 to 2006, a total of 153 mountain plover broods were monitored on the primary breeding habitats in eastern Colorado, USA; two shortgrass prairie habitats that were either occupied or unoccupied by black-tailed prairie dogs *Cynomys ludovicianus* and agricultural lands. Habitat quality hypotheses were tested using newly developed statistical applications to estimate survival of chicks and brood movement patterns.

3. Chick survival and brood movements were influenced by habitat. Chick survival over the 30-day brood-rearing period was substantially higher on nesting habitat of shortgrass occupied by prairie dogs compared with agricultural land and shortgrass unoccupied by prairie dogs. The rate of brood movement away from shortgrass with prairie dogs was lower than shortgrass without prairie dogs, but higher than agricultural lands for each year of the study.

4. This study suggests that complex processes influence how different habitats affect brood-rearing activity of mountain plovers. Even though broods moved off nesting habitat of shortgrass occupied by prairie dogs, this habitat had the highest survival rate and is highly important to mountain plover reproductive success.

5. *Synthesis and applications.* In order to develop effective conservation strategies, the provision of adequate breeding habitat should include information on patterns of habitat selection for all stages of the breeding cycle, including the nesting and dependent young periods. From a conservation perspective, understanding the habitat use of young birds is critical when population dynamics show great sensitivity to survival of young. Previous studies on mountain plovers have suggested that nest success is similar among shortgrass prairie habitats and agricultural lands. Thus, conservation measures that increase nest success may be ineffective for mountain plovers unless they are accompanied by measures promoting chick survival.

Key-words: brood movements, *Charadrius montanus*, chick survival, detection probability, habitat selection, mountain plover, multi-strata, precocial species, shorebirds.

Introduction

Interaction between habitat-specific demography and habitat selection may be a crucial component in population dynamics and regulation. The value of a habitat depends not only on the

current resources available and the ability to provide resources for some time in the future (Orians & Wittenberger 1991) but also the life stage of the individual. For example, in birds, the stage of the breeding cycle (i.e. nest and fledging) determines the value of a habitat. A habitat with high nest survival is not always the same type of habitat supporting the highest rate of fledging success. To complete the breeding effort successfully, habitats must support more birds as the breeding cycle advances to enhance the persistence of the population, decrease energetic costs of foraging, as well as reduce exposure to predators.

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Habitat use of fledgling birds, and its relationship to survival, is poorly understood for most avian species. From a conservation perspective, understanding the habitat use of young birds may be critical because population dynamics often show great sensitivity to survival of young (Anders *et al.* 1997; Colwell *et al.* 2007), although this depends on the life history of the species.

Habitat selectivity of young precocial species is usually determined by the attending parent(s) that lead their young to different habitats until they attain full independence. For example, in many precocial shorebirds, the parent(s) lead their chicks from the nest to different habitats where chicks feed, grow and fledge (e.g. Lengyel 2006; Colwell *et al.* 2007; Kosztolányi *et al.* 2007). There are several potential benefits that young may gain in moving to different habitats. First, they can be better protected from predators. Second, they may avoid competition with conspecifics (Lengyel 2006). Third, they may exploit better foraging resources. There are also costs such as increased chick mortality during extensive movements because of higher rates of starvation. Furthermore, habitats with more food resources may also have higher predation risks.

This study used newly developed quantitative methods to compare how habitat influenced survival of chicks and brood movement activity of a declining North American upland shorebird, the mountain plover *Charadrius montanus*. Habitats included the primary mountain plover breeding habitat in eastern Colorado, USA; agricultural land, shortgrass prairie occupied by prairie dogs and shortgrass prairie unoccupied by prairie dogs. Chick survival was estimated with an analytical method that accounts for imperfect detection of chicks. Brood movements were estimated using a multi-state model allowing for missing values (or data) in the encounter histories.

Habitat quality hypotheses were tested based on the ecology of this species. The distribution of adult plovers across eastern Colorado during the breeding season suggests that density on agricultural land is similar to density on shortgrass unoccupied by black-tailed prairie dogs *Cynomys ludovicianus* (hereafter referred to as grassland), but substantially lower than shortgrass occupied by black-tailed prairie dogs (hereafter referred to as prairie dog) (Tipton *et al.* 2009). Mountain plover chick survival was hypothesized to be the highest on prairie dog nest habitat. Knopf & Rupert (1999) reported that two of three broods that nested on grassland moved to an agricultural field within 2 km of the nest site. By contrast, Dreitz *et al.* (2005) suggested broods that nested on agricultural land moved to different habitats, and broods that nested on habitats other than agricultural land stayed on the nest habitat. Because studies on other shorebird species suggest that broods move to the habitat with the highest chick survival and stay at that habitat (Lengyel 2006; Schekkerman & Beintema 2007), I hypothesized that broods that nested on prairie dog habitat would tend to stay on their nest habitat and broods that nested on other habitats would tend to move to prairie dog habitat. Mountain plover chicks are nidifugous and feed themselves on a wide range of arthropods (Baldwin 1971; Knopf & Wunder 2006). Foraging conditions for

plover chicks may be affected by changes in food availability between habitats (Knopf 1998). No previous study has compared plover prey resources (i.e. arthropod populations) on different habitats. Prey availability of each habitat during the brood-rearing period is hypothesized to explain the observed patterns in chick survival and brood movement activity between habitats. Specifically, plover prey density and biomass on prairie dog nest habitat is predicted to be higher resulting in higher chick survival and movement to prairie dog habitat.

Explanatory variables relating to individual characteristics and temporal variation were included to explore the relevance of habitat quality in explaining patterns of chick survival and brood movements of mountain plovers. The mountain plover breeding system is described as double clutch with two clutches laid per pair per year; the first clutch is tended by the male and the second by the female (Graul 1973). Uniparental behaviour continues through the brood-rearing stage (Knopf & Wunder 2006). Dinsmore & Knopf (2005) found that chicks tended by females had higher survival than those tended by males. Therefore, the sex of the tending adult was included as a variable. In addition, yearly effect was included to explain temporal variability such as weather conditions and different groups of observers assisting each year of the study. This work provides new information on the relative roles played by different habitats in a highly fragmented landscape on the brood-rearing ecology of mountain plovers and will help land managers develop conservation agendas for this declining shorebird.

Materials and methods

FIELD SITE

The study area covered 21 500 km² in eastern Colorado, USA (see Supporting Information Fig. S1) on privately owned lands. Climate is characterized by low relative humidity, abundant sunshine, large daily temperature range and low average annual precipitation (~0.35 m) that mainly (70–80%) occurs during the growing season, April to September, largely from thunderstorm activity. The landscape is relatively flat and dominated by pastures of shortgrass prairie and dryland agricultural fields. The two shortgrass prairie habitats were vegetated by low-growing buffalograss *Buchloe dactyloides* and blue grama *Bouteloua gracilis*. Shortgrass that was grazed to varying degrees by domestic ungulates, primarily cattle, was defined as grassland and that grazed by a native herbivore, the black-tailed prairie dog, was defined as prairie dog. Agricultural land was comprised of fields of dryland crops, primarily wheat *Triticum aestivum* L. and sorghum *Sorghum bicolor* L. and fallow strips with varying structure of crop stubble.

Specific field sites were selected such that a habitat was juxtaposed < 2 km from one of the other two habitats to permit brood movements between habitats. Boundaries distinguishing agricultural fields from the other habitats were easy to determine visually. Defining the boundaries between prairie dog and grassland was problematic. When adjacent to grassland, prairie dog habitat was defined as the prairie dog colony plus a 0.40 km buffer based on similarities in vegetative structure (e.g. height, amount of bare ground). The total area of each habitat included in the study varied between years

but followed a general pattern of agricultural land \approx prairie dog \leq grassland.

FIELD DATA COLLECTION

From April to August 2004–2006, data were collected on mountain plover brood-rearing ecology. Mountain plover chicks leave the nest within 3 h of the last egg hatching, and by the end of their first day, chicks appear capable of catching small arthropods (Graul 1973). Mountain plover chicks fledged at 33–36 days post-hatch (Graul 1975; Miller & Knopf 1993). However, the brood-rearing period was defined from hatch to 30 days post-hatch to avoid potential premature fledging of chicks. Monitored broods were from known nests located < 2 km from one of the other two habitats of interest, allowing potential movement between habitats.

Plover prey resources

Pitfall traps were used to measure prey density and biomass of surface-active arthropods (Work *et al.* 2002). Prey sampling was in known areas of plover nesting activity at the same nine sites (three replicates per the three habitats) each year. Sampling sites were selected at random but restricted to one site per habitat patch. A trapping line transect grid (Lukacs *et al.* 2004b) of 20×10 m² with 60 pitfall traps at ≥ 0.5 -m intervals (see Supporting Information Fig. S2) was installed at each site. Individual pitfall traps were placed < 0.1 m of the target location. Pitfall traps were 16-oz Solo[®] plastic cups (95 mm diameter, 115 mm depth) that were buried in the soil with the top of the cup flush with the soil's surface.

The nine grids were installed 1 week prior to field sampling. During sampling, the traps were filled with ~ 200 ml of water and < 1 ml of liquid dishwashing detergent to reduce the surface tension of the water and prevent arthropods from escaping. Sampling was conducted between the hours of sunrise ($\sim 05:00$ hours MST) and 11:00 hours MST because plovers are most effective at foraging early in the morning (Knopf & Wunder 2006). The contents of each pitfall trap were identified to order and family; sorted by life stage; and dried at 60 °C for 48 h to obtain dry biomass of each trap to the nearest 0.01 mg. The stomach contents from three mountain plover chicks yielded prey items < 15 mm in length (Baldwin 1971). Flying arthropods were rare prey items because chicks are not capable of flight until 33–36 days (Graul 1975; Miller & Knopf 1993). Hence, mountain plover chick prey items (hereafter, simply prey items) were defined as arthropods that were < 15 mm in length and not capable of flight.

Monitoring brood-rearing activity

Lightweight 1.8 g radio transmitters (A2450, Advanced Telemetry Systems, Inc.) were fitted to nest-tending adults 1–5 days prior to hatching. Adults with nests < 2 km from one of the other two habitats were captured with a walk-in trap placed over the nest. Transmitters were affixed by applying a light coating of waterproof epoxy (i.e. cyanoacrylate glue) and sliding it under the upper layer of mantle feathers so that the transmitters was positioned between feathers (Dreitz *et al.* 2005). Transmitters were likely to be shed during moulting prior to autumn migration. The battery life of transmitters was expected to be ≥ 56 days. Additionally, a feather sample was collected from each adult for sex determination using DNA analysis.

After hatching, adults were located every 24–48 h to record their location, habitat and the number of chicks present until chicks were fledged at 30 days post-hatch. Observations were < 30 min, dependent on the age of chicks, with less time spent observing younger individuals due to their vulnerability.

STATISTICAL ANALYSIS

Plover prey resources

An approach based on distance sampling with trapping line transects was used to calculate the density of plover prey availability (Lukacs *et al.* 2004b). Trapping line transects are passive in that individuals (or groups) are detected by entering a trap whose distance from the centre line is known. The detection function is estimated from information obtained on the perpendicular distance from the centre line to a trap off the centre line. Trap density is the highest on the centre line and decreases with increasing distance away from the centre line. The density estimator for trapping line transects was:

$$\hat{D} = \frac{n}{2wL\hat{P}_a}$$

where n is the number of different individuals trapped, w is the width of the trapping grid, L is the length of the grid and \hat{P}_a is the estimated probability that an individual is trapped given area a . The variance of the estimated density was:

$$\widehat{\text{var}}[\hat{D}] = \hat{D}^2 \{ \{ \text{cv}(n) \}^2 + \{ \text{cv}[\hat{P}_a] \}^2 \}.$$

Program DISTANCE 5.0 (Thomas *et al.* 2006) was used to estimate the prey density. Distance sampling uses a set of six models each composed of a key function or general shape function to fit the detection function, and a nonparametric flexible form called a 'series expansion' that adjusts the key function (Thomas *et al.* 2006). The number and arrangement of pitfall traps for the trapping line transect grid (see Supporting Information Fig. S2) was based on simulations using the hazard rate key function with a simple polynomial expansion series model. This same model was used to produce density estimates of plover prey per 100 ha for each habitat per year of the study.

The dry weight of each pitfall trap was computed to obtain a measure of biomass. Data were grouped across sampling days such that there were 18–27 replicates (three grids \times six or nine sampling days) per habitat for each year. The mean and standard error was calculated for each habitat and year in SAS PROC MEANS (SAS Institute 2003).

Chick survival

Chick survival was calculated using a likelihood-based extension of the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) in which information collected on the attending adult and its chicks is used to estimate survival of dependent young (Lukacs *et al.* 2004a). The approach requires that the attending adult be uniquely marked, and that the mark be read without error each time the adult is re-sighted. The young are not required to have any form of mark. The parameters of interest include the probability of survival of an individual chick from time i to time $i + 1$ given the chick is alive at time i and remains on the study area, ϕ , and the probability that a chick will be re-sighted given it is alive and the adult was re-sighted at time i , p . Because of all possible outcomes of ϕ for a chick within a brood, ϕ becomes a matrix, Φ :

$$\begin{bmatrix} \phi_i^m \binom{m}{m-1} \phi_i^{m-1} (1-\phi_i) \binom{m}{m-2} \phi_i^{m-2} (1-\phi_i)^2 \dots \binom{m}{0} (1-\phi_i)^m \\ 0 & \phi_i^{m-1} & \binom{m-1}{m-2} \phi_i^{m-2} (1-\phi_i) \dots \binom{m-1}{0} (1-\phi_i)^{m-1} \\ 0 & 0 & \phi_i^{m-2} & \dots & \binom{m-2}{0} (1-\phi_i)^{m-2} \\ \vdots & \vdots & 0 & \ddots & \vdots \\ 0 & 0 & \dots & 0 & 1 \end{bmatrix}$$

where m is the maximum number of chicks in a brood. The rows represent the number of chicks alive at encounter occasion i and the columns represent the number of chicks alive at $i + 1$. The possible outcomes of p are handled such that \mathbf{p}_i is:

$$\begin{bmatrix} p_i^m & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & & \\ 0 & & \ddots & & \vdots \\ \vdots & & & & \\ 0 & & & & 0 \end{bmatrix}, \text{ if } h_i = m_i,$$

$$\begin{bmatrix} \binom{m}{m-1} p_i^{m-1} (1-p_i) & 0 & 0 & \dots & 0 \\ 0 & p_i^{m-1} & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \\ \vdots & & \ddots & \ddots & \vdots \\ 0 & & & & 0 \end{bmatrix}, \text{ if } h_i = m-1, \dots,$$

$$\begin{bmatrix} 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & \dots & & 1 & 0 \\ 0 & 0 & \dots & 0 & 1 \end{bmatrix}, \text{ if } h_i \text{ is unobserved } (.)$$

where h_i is the number of chicks seen at each sampling occasion for a given brood, either 0, 1, 2, ..., m , or '.'. A '.' represents a brood that was not sampled on a given occasion differing from a '0' in which a brood was sampled by observing the adult but no chicks were detected. Because data are obtained on individual chicks within a brood, this approach allows for an estimation of chick survival, not brood survival.

The likelihood function is proportional to a multi-nomial probability mass function

$$L(\phi, p | n, \mathbf{h}) \propto \prod_{i=1}^n P[\mathbf{h}_i].$$

The likelihood function was optimized to obtain the maximum likelihood parameter estimates in program R (R Development Core Team 2007).

Using the above approach, a suite of models were developed to test the specific habitat quality hypotheses examining brood-specific effects on individual chick survival (see Supporting Information Table S1). For all models, p was either constant (.) or varied by year (year). While the probability of detecting a chick is conditional on detecting the adult, the data used in the analysis are dependent on locating the attending adult using radio telemetry. Thus, it is unlikely that p would vary by habitat or other environmental covariates. The inclusion of year accounts for potential differences between the different observers collecting data each year.

For ϕ , the effects of nest habitat, prey density and biomass within nest habitat, sex of the adult and year were investigated.

The model set explicitly examined if nest habitat or characteristics of nest habitat influenced survival of chicks. The sex of the adult was included because it has been reported to influence chick survival of mountain plovers in other parts of the species' range (Dinsmore & Knopf 2005). The effect of year was included because chick survival for most avian species exhibits annual variation. The model set also included additive or multiplicative combinations of the different factors.

Model selection and inference was based on information-theoretic methods and scored using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham & Anderson 2002). The models were ranked and compared in terms of their ability to explain variation in the empirical data using ΔAIC_c and AIC_c weights (Buckland *et al.* 1997; Burnham & Anderson 2002). The ΔAIC_c for a given model is the difference in AIC_c between the best approximating model and all other models (Burnham & Anderson 2002). Further, to better interpret the relative likelihood of a given model over a set of models, models are normalized (by summing to 1) to yield a set of AIC_c weights. Evidence ratios were computed based on the weight of the best approximating model over the next best model (Burnham & Anderson 2002).

Chick survival was computed over the 30-day brood-rearing period of interest as: $\phi_{30\text{-day}} = \phi_{\text{daily}}^{30}$ where ϕ_{daily} is the daily estimate based on the best model. The top model carried most of the AIC_c weight; so, this procedure provides a reasonable estimate of $\phi_{30\text{-day}}$. Based on a delta approximation, the variance of the estimate $\phi_{30\text{-day}}$ follows:

$$\widehat{\text{var}}[\phi_{30\text{-day}}] = (30\phi_{\text{daily}}^{29})^2 \widehat{\text{var}}[\phi_{\text{daily}}].$$

Movement probabilities

A multi-state (or multi-strata) modelling approach was used to investigate daily brood movements. This approach is an extension of the CJS (Cormack 1964; Jolly 1965; Seber 1965) live captures model extended to multiple states (Hestbeck *et al.* 1991; Brownie *et al.* 1993; Schwarz *et al.* 1993). States can be geographical areas, physiological states or behavioural status. In this study, states refer to the different habitats. A daily brood movement event (or transition) was defined as the movement from one habitat to a different habitat within a 24-h period.

The parameters of interest in this multi-state analysis include p_i^s , the probability of re-sighting a brood in state s at time i , and ψ_i^{rs} , the probability that a brood in state r moves to state s at the end of the interval starting at time i , conditional on the brood remaining alive and available for re-sighting. An additional parameter included in the multi-state modelling approach is the probability of survival during interval i on state r , ϕ_i^r . For this study, ϕ_i^r is the probability of brood survival during interval i on state r . Because the study focused on chick survival and not brood survival, ϕ_i^r was constrained to be constant across all strata, treating ϕ as a nuisance parameter rather than a parameter of interest.

States were defined as the three habitats; agricultural fields (A), grassland (B) and prairie dog (C), '0' represents a sampled but undetected brood, and '.' represents a brood that was not sampled on a given occasion (i.e. missing value). For example, an encounter history such as

AC · 0B

indicates a brood initially observed on agricultural land that moved to and was re-sighted on prairie dog during the second

occasion, was not sampled during the third occasion, was sampled but not re-sighted during the fourth occasion, then was re-sighted on grassland during the last occasion.

A set of candidate models was developed to test the habitat quality hypotheses on daily brood movement probabilities (see Supporting Information Table S2). Similar to the chick survival analysis, p was modelled as constant or varying by year and ψ was modelled as a function of the habitat of location (not necessarily the nest habitat), prey density and biomass within the nest habitat, sex of the adult, and year, or additive combinations. AIC_c was used for model selection and inference as described above (see *Statistical Analysis: Chick Survival*). The multi-state analysis was conducted in program MARK (White & Burnham 1999).

The probability of at least one movement from one habitat to a different habitat was computed over the 30-day brood-rearing period as: $\psi_{30\text{-day}} = 1 - (1 - \psi_{\text{daily}})^{30}$ where ψ_{daily} is the daily movement probability. Because the best approximating model contained all of the AIC_c weight (1.00), the daily movement estimates from this model were used to compute ψ_{daily} . The variance is based on a delta approximation as:

$$\widehat{\text{var}}[\psi_{30\text{-day}}] = (-30(1 - \psi_{\text{daily}})^{29})^2 \widehat{\text{var}}[\psi_{\text{daily}}].$$

Results

PLOVER PREY RESOURCES

Pitfall trapping

Data were collected on prey items in 12 960 pitfall traps. In 2004, sampling occurred only twice (May and July) because substantial rain hindered access to the grids in mid-June. Of the 12 960 pitfall traps, 4.8% (621 pitfall traps) contained no plover prey items. A total of 117 501 plover prey items were collected: 26 743 (22.8%) on agricultural land, 52 501 (44.7%) on grassland and 38 257 (32.6%) on prairie dog. Species in the Order Hymenoptera, Family Formicidae (i.e. ants) comprised 50.5% (59 485 prey items) of the total prey items. The Order Coleoptera comprised the second highest number of total prey items with 31 088 prey items (26.8%). Sap beetles (Family Nitidulidae) comprised 70.9% (22 055 prey items) of this Order. The largest number of the prey items collected on agricultural land were species in the Order Coleoptera (41.5%, 11 089 prey items of 26 743) and on grassland and prairie dog were species in the Order Hymenoptera (63.8%, 33 487 prey items of 52 501 and 53.3%, 20 400 prey items of 38 257 respectively).

Density and biomass

To estimate density, prey items were clustered by Family for each pitfall trap for a total of 40 670 prey observations: 13 253 observations on agricultural land, 13 920 on grassland and 13 515 on prairie dog. The estimates of prey density varied among habitats and years (Fig. 1a). Agricultural land had less variation in density across years than grassland or prairie dog (Fig. 1a). Biomass of plover prey varied among habitats and increased each year of the study (Fig. 1b). The point estimates

for biomass and density of prey items per habitat and year were used as covariates in the chick survival and the brood movement analyses.

PLOVER BROOD-REARING ACTIVITY

A total of 153 adults with broods were monitored (Table 1). Fewer broods from grassland nest habitat ($n = 20$ broods) were monitored than broods from agricultural ($n = 66$ broods) and prairie dog nest habitat ($n = 67$ broods). The effort to locate nests was the highest on grassland; therefore, low numbers of nests on grassland may have been due to low reproductive effort on this habitat during the study. More broods were tended by males ($n = 79$ broods) than females ($n = 48$ broods); this did not differ by year and nest habitat except for on prairie dog in 2006 in which an equal number of broods were tended by males and females (Table 1). The sex of 26 adults tending to a brood was unknown due to the lack of an appropriate sample for DNA analysis. At least 43 chicks from 28 broods (17 broods fledged at least one chick, seven broods fledged at least two chicks and four broods fledged at least three chicks) survived from hatch to 30-day post-hatch (Table 1).

Of the 153 broods monitored, 38 broods (25%) moved off the nest habitat at least once (Table 1). The number of broods that moved were similar for each of the three habitats but was higher in 2006 than in 2004 and 2005 (Table 1). Of the 38 broods that moved from their nest habitat, 76% ($n = 29$ broods) were observed most often on their nest habitat and averaged 2.79 (SD 2.12) movement events suggesting these

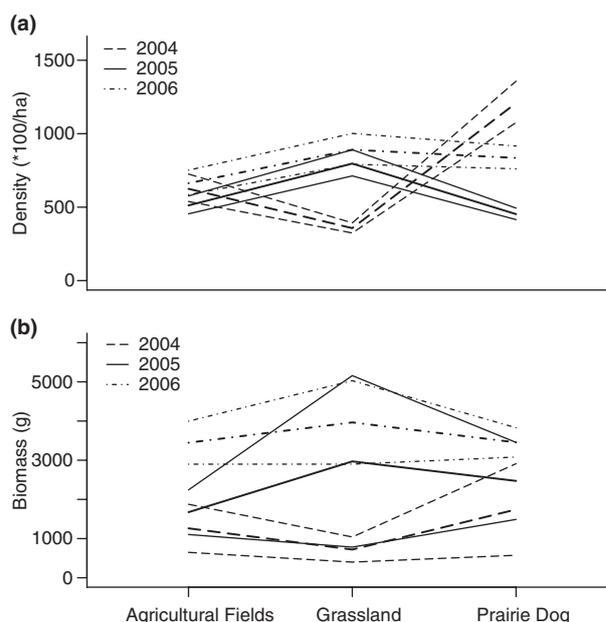


Fig. 1. Estimates of density (a) and biomass (b) and 95% confidence intervals for mountain plover prey items on agricultural fields, grassland and prairie dog colonies in Colorado from 2004 to 2006. Estimates are dark shaded; 95% confidence intervals are light shaded.

Table 1. Summary of mountain plover *Charadrius montanus* broods monitored in Colorado, USA from 2004 to 2006

	Year			Total
	2004	2005	2006	
Broods monitored				
Nested on agricultural lands	21	19	26	66
Males	15	7	15	37
Females	5	4	11	20
Unknown	1	8	0	9
Nested on grassland	5	6	9	20
Males	4	4	4	12
Females	1	1	2	4
Unknown	0	1	3	4
Nested on prairie dog colonies	17	38	12	67
Males	10	15	5	30
Females	5	14	5	24
Unknown	2	9	2	13
Broods that fledged chicks	10	14	4	28
Broods moved from nest habitat	6	8	24	38
On agricultural fields	1	2	8	11
On grassland	2	2	7	11
On prairie dog colonies	3	4	9	16

broods moved back and forth from their nest habitat. The average age of chicks at the first movement event occurred when chicks were slightly older in 2005 (9.25 days post-hatch, SD 7.21) than in 2004 (4.67 days post-hatch, SD 5.40) and in 2006 (4.88 days post-hatch, SD 4.65).

Chick survival

Based on AIC_c, the most parsimonious model that best explained the data was a model with chick survival differing among nest habitats and re-sighting probability differing by year (Table 2, also see Supporting Information Table S1). The results also indicated that differences in chick survival among nest habitats were greater than can be explained by our measures of prey density and biomass within the nest habitat, year or sex of the tending adult. In addition, the best approximating model contained most of the AIC weight (87%) compared with the next best model (8%) (Table 2, also see Supporting Information Table S1) and the evidence ratio suggests that the

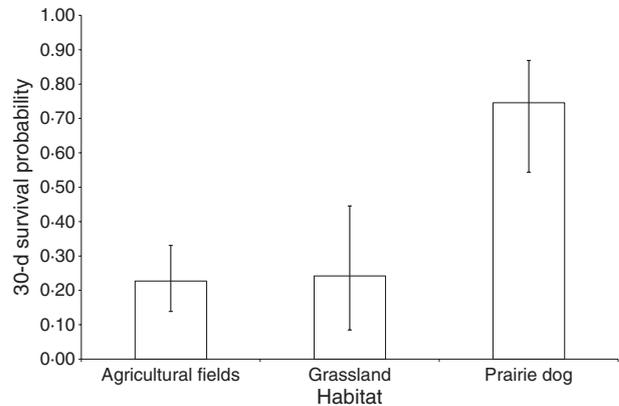


Fig. 2. Estimates of 30-day chick survival and 95% confidence intervals for mountain plovers nesting on agricultural fields, grassland and prairie dog colonies in Colorado from 2004 to 2006. Estimates are based on the top model in which chick survival differed among nest habitats and re-sighting probability differed by year

best approximating model was 10 times more likely than the second best model.

Daily chick survival estimates ranged from 0.95 (CI 0.93–0.96) for chicks hatched on agricultural land and grassland to 0.99 (CI 0.98–1.00) for chicks hatched on prairie dog. Taking these estimates over the 30-day brood-rearing period, substantial differences in chick survival exist between chicks from prairie dog nest habitat and chicks from nests on other habitats (Fig. 2). Thirty-day chick survival for prairie dog nest habitat (0.75, CI 0.54–0.87) is approximately three times higher than agricultural nest habitat (0.23, CI 0.14–0.33) and grassland nest habitat (0.24, CI 0.08–0.45) with no overlap in 95% confidence intervals. Re-sighting probabilities of individual chicks decreased through the years from 0.51 (CI 0.46–0.56) in 2004 to 0.25 (CI 0.26–0.36) in 2006.

Movement probabilities

The model selection criterion suggested that daily movement probabilities were influenced by the additive effects of habitat and year, and re-sighting probabilities were affected by year

Table 2. Summary of model selection results for mountain plover chick survival and brood movement activity in Colorado, USA, 2004–2006

	Model	K†	AIC _c ‡	ΔAIC _c	w _i §
Chick survival	$\phi(\text{habitat})p(\text{year})$	6	2497.62	0.00	0.87
	$\phi(\text{year} + \text{prey density})p(\text{year})$	7	2504.14	6.52	0.08
	$\phi(\text{year} + \text{habitat})p(\text{year})$	8	2507.00	9.38	0.05
	$\phi(\text{sex of tending adult})p(\text{year})$	5	2517.22	19.61	0.00
Brood movement	$\psi(\text{habitat} + \text{year})p(\text{year})$	12	1634.13	0.00	1.00

Models with a ΔAIC_c < 20 units are presented in ascending by AIC_c, with ΔAIC_c indicating the difference between each model and the model with the lowest AIC_c value. For chick survival, apparent survival (ϕ), included the effects of habitat, year, sex of the tending adult, and plover prey density. Re-sighting probability (p) included the effect of year. For brood movement, brood movement (ψ) included the effects of habitat and year and re-sighting probability (p) included the effect of year.

†The number of parameters.
‡Akaike's information criteria.
§Akaike weight.

(Table 2, also see Supporting Information Table S2). The top model contained 100% of the AIC weight (Table 2, also see Supporting Information Table S2). Models containing the effects of prey density or biomass within the nest habitat or sex of the tending adult ranked substantially lower, $> 32 \Delta AIC_c$ units, from the best approximating model (see Supporting Information Table S2).

Daily movement probabilities for each habitat per year were relatively small ranging from 0.00 to 0.12. The 30-day brood-rearing period estimates suggest that plover broods on grassland were more likely to leave grassland and move, at a similar rate, to either agricultural land or prairie dog (Fig. 3, also see Supporting Information Table S3). Movement probabilities from agricultural land to other habitats had the lowest estimates each year, but these estimates were not significantly different from the probabilities of moving from prairie dog to other habitats. Further, the results suggest that broods moved among habitats more frequently in 2006 than in either 2004 or 2005 (Fig. 3, also see Supporting Information Table S3). Re-sighting probabilities for broods, not individual chicks as in the chick survival analysis, were relatively high ranging from 0.88 to 0.98.

Discussion

The habitats used by mountain plover broods strongly influenced chick survival and movement patterns. Similar findings have been observed in other shorebirds with precocial young (e.g. Lengyel 2006; Colwell *et al.* 2007; Kosztolányi *et al.* 2007; Schekkerman & Beintema 2007). Daily chick survival estimates for each nest habitat are within the range of those reported in past studies for mountain plovers (Miller & Knopf

1993; Knopf & Rupert 1996; Lukacs *et al.* 2004a; Dinsmore & Knopf 2005). Studies on other shorebird species suggest that broods move to the habitat with the highest chick survival and stay at that habitat (Lengyel 2006; Schekkerman & Beintema 2007). By contrast, some mountain plover broods moved away from the nest habitat with the highest chick survival. Further, broods moved off all the habitats included in the study, similar to findings by Knopf & Rupert (1999), and brood movement was not dependent on the type of habitat as suggested by Dreitz *et al.* (2005). Prey availability of a habitat has been suggested to influence both chick survival and brood movements of shorebirds (Lengyel 2006; Colwell *et al.* 2007; Kosztolányi *et al.* 2007; Schekkerman & Beintema 2007), but this was not supported in this study.

PREY AVAILABILITY

Contradictory to the hypothesis, density and biomass of plover prey resources within the nest habitat did not explain patterns of mountain plover chick survival or brood movements among habitats. Although prey resources may reflect habitat quality, direct measurement of prey resources is challenging. Sampling of arthropod populations within and between habitats is complicated by spatial and temporal variation in prey abundance (Smith & Rotenberry 1990). Prey densities on grassland and prairie dog nest habitats varied more between years than between densities on agricultural nest habitat. This result supports the hypothesis that the distribution of prey resources can be aggregated, and these aggregations shift during the breeding season and between years as resources fluctuate (Smith & Rotenberry 1990; Schekkerman & Beintema 2007). Prey biomass also varied between nest habitats and increased on each nest habitat during the study. Variation in biomass may be a result of temporal changes in arthropod life cycles including those dictated by either long- or short-term weather conditions or habitat-specific management (Vickery *et al.* 2001). The study area experienced a severe drought in 2002. The observed increasing yearly trend in prey biomass may be in response to this weather event. Finally, the measures of density or biomass of prey used in this study may be poor predictors of habitat quality for mountain plover chicks. Habitat quality may be more influenced by a combination of factors, including predation pressures and natural disturbances associated with weather.

CHICK SURVIVAL AND BROOD MOVEMENTS

This study supports the relative importance of habitats occupied by prairie dogs to mountain plover reproductive success. Breeding habitat for mountain plovers is associated with areas of high disturbance such as those intensively grazed by native or domestic herbivores, recently burned areas and agricultural lands (Knopf & Wunder 2006). As predicted, adults nesting on prairie dog habitat were three times more likely to fledge chicks (0.75, CI 0.54–0.87) than adults nesting on agricultural land (0.23, CI 0.14–0.33) and grassland (0.24, CI 0.08–0.45). This result suggests that habitats occupied by prairie dogs may be providing

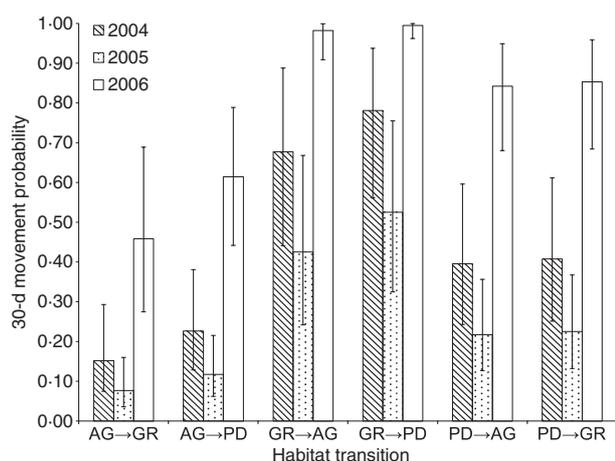


Fig. 3. Estimates of mountain plover 30-day brood movement probabilities and 95% confidence interval in Colorado from 2004 to 2006. A movement event is defined as moving from one habitat to a different type of habitat within a 24-h period. The habitats are defined as agricultural fields (AG), grassland (GR) and prairie dog colony (PD). Estimates are based on the top model in which daily movement probabilities were influenced by the additive effect of habitat and year, and re-sighting probabilities differed by year.

the disturbance needed for mountain plovers to successfully raise chicks. In terms of breeding success, Dreitz & Knopf (2007) did not find that habitat influenced nest success when categorized as either agricultural land or grassland with or without prairie dogs. Habitat-related reproductive success between nesting and chick survival suggests that mountain plovers may incorrectly assess nest sites on agricultural lands and grassland, which may function as ecological traps given the low rate of chick survival on these habitats. Similar findings have been suggested for other shorebird species (Székely 1992; Lengyel 2006).

It is unknown why mountain plover broods moved away from prairie dog habitat, even though this habitat had the highest success in fledging chicks when used as a nesting habitat. Brood movement can have extensive costs to chicks and the parent. A total of 30 broods in this study were censored due to mortality of the tending adult ($n = 11$), or where the radio transmitter was found but the fate of the adult could not be confirmed ($n = 19$). Of the adult mortalities, seven were from broods that stayed on their nest habitat, and four from broods that moved to different habitat. While the sample sizes are small, our results suggest that mortality of the tending adult, and most probably the chicks, does not increase as a result of movement to different habitats. In fact, movement to a different habitat may increase survival of chicks and the parent. The brood movement findings from this study suggest that complex processes influence how different habitats affect brood-rearing activity of mountain plovers and further study on factors influencing mountain plover brood movement is warranted.

Beyond the habitat quality hypotheses, the sex of the attending adult and yearly variability were also included to potentially explain the observed patterns in both chick survival and brood movement. On breeding grounds in Montana, USA, mountain plover broods tended by females had higher chick survival rates than males (Dinsmore & Knopf 2005). By contrast, this study did not find that the sex of the attending adult influenced chick survival. Different factors, such as habitats (Colorado shortgrass vs. Montana mixedgrass), breeding densities or landscape configuration may be contributing to these spatial differences between breeding populations. Additionally, sex of the tending adult did not influence mountain plover brood movement which has been observed in the Kentish plover *Charadrius alexandrinus* (Kosztolányi *et al.* 2007). The reason that year of the study influenced brood movements but not chick survival is unknown. There were many differences between the study years, such as weather conditions. For example, frequent light rain events occurred throughout the brood-rearing period during 2006, when relatively high levels of brood movement between habitats were observed. During 2004 and 2005, weather events were less frequent but more severe including hailstorms and flooding, causing mortality of chicks and, consequently, lower rates of brood movement occurred.

This study is the first to quantify important aspects of the brood-rearing period of mountain plovers among the most commonly used habitats. While prey density and biomass did not influence chick survival or brood movements, other physical or ecological characteristics of the different habitats may influence these reproductive parameters. Differences in predation

pressure between habitats have been demonstrated to influence chick survival and brood movements in many species. Species exposed to predators can change their habitat use by moving to habitats with lower encounters with predators or they can aggregate in groups using various defence mechanisms to fend off predators. Competition also plays a role in chick survival and brood movements in shorebirds (Lengyel 2006; Kosztolányi *et al.* 2007). Intraspecific competition among pied avocets *Recurvirostra avosetta* for brood-rearing territories is thought to cause brood movement to less suitable habitats (Lengyel 2006). Similar behaviour may be occurring with mountain plover broods, especially when the density of broods in a habitat patch exceeds the availability of resources.

CONSERVATION IMPLICATIONS

An important finding of this study is that conservation strategies aimed at increasing nest success may be ineffective for mountain plover unless they are accompanied by measures promoting chick survival. For some shorebird species, fledging of chicks appears to be more closely related to population dynamics than nesting success (Lengyel 2006; Colwell *et al.* 2007). The three habitats evaluated in this study are thought to be highly suitable for nesting success (Dreitz & Knopf 2007). However, the results presented here support the ecological trap hypothesis in that seasonal changes can decrease the suitability for fledging of two of the three nesting habitats, thus reducing the chances of successful reproduction. However, further assessment of brood-rearing ecology on a larger spatial scale is necessary to confirm this result. The conservation of mountain plovers should concentrate on habitats where survival of chicks is the highest, i.e. shortgrass prairie occupied by prairie dogs, to determine which particular attributes of these habitats (e.g. vegetation structure, predation pressure and prairie dog behaviour) influence reproductive success.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Summary of model selection results for Mountain Plover chick survival.

Table S2. Summary of model selection results for Mountain Plover brood movements.

Table S3. Parameter estimates of Mountain Plover 30-day brood movement probabilities between habitats.

Fig. S1. Map illustrating the general study area in eastern Colorado, USA.

Fig. S2. Schematic diagram and photograph of field application of trapping line transect grid.

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