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Mountain Plover Population Responses to Black-Tailed Prairie Dogs in Montana

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The finite rate of population change, lambda ($\lambda$), is often of fundamental importance to ecologists interested in assessing population status. Estimates of lambda can show that a population is increasing ($\lambda > 1$), stable ($\lambda = 1$), or declining ($\lambda < 1$) and provide a more formal means of interpreting estimates of population size. Understanding these rates becomes even more important for rare or declining species that require immediate intervention to rescue them from further declines or extinction.

The traditional method of estimating $\lambda$ has been with the use of Leslie projection matrices (Leslie 1945, Caswell 2001). Under this method, measures of average age-specific survival and fecundity are used to project population growth over a specified period. However, this method has problems. The most important flaw is that the rates that are often used represent averages over a specified time period, so predicted values of $\lambda$ are also averages and may not be reasonable predictors of future trends. Additionally, estimates of $\lambda$ from projection matrices may be biased downward if there is substantial emigration, particularly among juvenile age classes (Franklin et al. 1996).

Pradel (1996) introduced a reparameterization of the Jolly-Seber model to estimate the finite rate of population change ($\lambda$) in addition to apparent survival ($\phi$) and conditional capture probability ($p$). Unlike the Leslie projection matrix, this method directly accounts for internal (reproduction and mortality) and external (immigration and emigration) influences on the population of interest and is an improvement because $\lambda$ is estimated directly from the data.

Mountain plovers are a local and declining shorebird of the western Great Plains (Knopf 1994). Perceived declines led to a proposal to list them as a Threatened species in 1999 (U.S. Department of the Interior 2002). Rigorous assessment of plover status and trends at key breeding areas is needed and will provide a better understanding of local population dynamics and help future conservation efforts for this species.

We provide estimates of annual rates of population change ($\lambda$) from 1995 to 1999 for a population of mountain plovers in southern Phillips County, Montana.
Mountain Plovers and Prairie Dogs in Montana

County, Montana. Southern Phillips County is thought to contain the largest breeding population of plovers in Montana and one of the largest in North America (Knopf and Miller 1994). We discuss population trends at this site in light of the total size of this population (Dinsmore et al. 2003) and changes in the area occupied by black-tailed prairie dogs. We then comment on the status and future outlook for mountain plovers at this key breeding site, and we identify several aspects of their biology needing further study.

STUDY AREA

We studied mountain plovers on a 3,000-km² area in southern Phillips County in north-central Montana (47°40′-47°55′N, 107°35′-108°30′W; Fig. 1). The study area was 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 2,250 km² of the study area was 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 was a mixed-grass prairie with sagebrush flats bordering the southwestern edge of the Prairie Pothole Region (Knowles et al. 1982, Olson and Edge 1985). Predominant vegetation included big sagebrush (Artemisia tridentata), silver sagebrush (Artemisia cana), greasewood (Sarcobatus vermiculatus), yellow sweetclover (Melilotus officinalis), green needlegrass (Stipa viridula), and western wheatgrass (Agropyron smithii). Active black-tailed prairie dog colonies contained variable amounts of bare ground interspersed with sparse vegetation that included fringed sagewort (Artemisia frigida), plains prickly pear (Opuntia polyacantha), blue grama (Bouteloua gracilis), needle-and-thread grass (Stipa comata), and Sandberg bluegrass (Poa secunda), with fewer grasses generally present on the older colonies. Mean annual precipitation near the center of the study area was 33 cm, most of which fell from May to July (D. Veseth, Veseth and Veseth Inc., personal communication). Mean elevation was approximately 930 m.

We studied mountain plovers exclusively on or adjacent to active black-tailed prairie-dog colonies because previous research found that mountain plovers preferentially used such sites in Montana (Knowles et al. 1982, Knowles and Knowles 1984). Prairie-dog numbers fluctuated considerably in southern Phillips County, mainly as a result of outbreaks of sylvatic plague, an epizootic (Barnes 1993), although recreational shooting may have a negative impact on some of the smaller prairie-dog colonies (Vosburgh and Irby 1998). Prairie dogs have rapidly recovered from the last major plague outbreak in 1992-96. Colony areas were reduced by about 80% during this outbreak, but they have since increased from 1,371 ha in 1995 to 5,071 ha in 2000 (J. Grensten, Bureau of Land Management, personal communication; Fig. 2). Inactive colonies, mostly the result of plague outbreaks, were not included in this total because habitat on such colonies rapidly became unsuitable for plovers, often within a matter of a few weeks.

METHODS

Capture and Marking

We studied mountain plovers from 20 May to 20 July during 6 breeding seasons (1995-2000). We systematically searched active prairie-dog colonies within the study area ≥3 times each year. On these searches we slowly drove a vehicle across each colony and periodically stopped to scan for plovers. We watched individual adult birds from a distance until they returned to a nest. Once we located a nest, we trapped the adult immediately with a walk-in, wire-mesh trap placed over the nest, and we then banded the bird with a unique
Estimating Population Trends ($\lambda$)

We estimated the finite rate of population change ($\lambda$) and recruitment ($f$) using the Pradel lambda models (Pradel 1996) in program MARK (White and Burnham 1999). We estimated annual apparent survival and population size earlier using the robust design (Dinsmore et al. 2003); our focus was only on estimates of $\lambda$ and $f$. Models to estimate $\lambda$ directly from a robust design study have not been developed, so we were forced to slightly modify our approach to estimating $\lambda$ and $f$ with this model.

We summarized releases and live resightings of banded plovers in encounter history format with 6 encounter occasions, 1 for each year of the study. We only used information from adult plovers, which included all birds first banded as adults and all juveniles that were subsequently resighted as adults. Using this approach, we estimated the annual rate of the breeding adult population change ($\lambda$) for 5 years (1995–1999) and recruitment ($f$) for 5 years (1996–2000).

Our general approach to modeling $\lambda$ and $f$ followed Lebreton et al. (1992) and Burnham and Anderson (2002). We first developed a list of a priori factors influencing each parameter ($\phi$, $p$, $f$, $\lambda$), and we then used this information to define a set of candidate models.

The Pradel models allowed the simultaneous estimation of apparent survival ($\phi$) with capture probability ($p$) and the finite rate of population change ($\lambda$) or recruitment ($f$). Because there was only a single encounter occasion per year, we could not estimate the recapture probability ($c$). Under this model, population change was estimated as:

$$\hat{\lambda}_t = \frac{N_{t+1}}{N_t}$$

where $N_t$ represented the population size at some time $t$. Between times $t$ and $t + 1$ the population changed as a function of births, deaths, emigration, and immigration. Thus, changes in $\lambda$ were a function of apparent survival, recruitment, and movement.

To estimate $\lambda$ using the Pradel model, we had to model annual apparent survival and initial capture probability correctly. For mountain plovers, we modeled apparent survival ($\phi$) as year-specific. Because we believed $\lambda$ changed annually, it made sense to also allow survival to vary annually, even though we suspected yearly differences in adult survival were small (Dins-
more et al. 2003). For comparison, we also included a single model where apparent survival was constant across years.

The initial capture of mountain plovers occurred by either physical capture (p) or resighting (r), and we knew from earlier work that the probability of physical capture was much lower than resighting probability (Dinsmore et al. 2003). In an earlier analysis, we showed that models where \( p = r + C \), where C was some constant, received the best support (Dinsmore et al. 2003). Limitations in the structure of the Pradel model prohibited modeling p and r separately, so we were forced to model all initial captures with probability p. We considered 2 constraints on capture probability: We let it be constant across years \([p(\cdot)]\) and allowed it to vary by year \([p(t)]\). Because differences in yearly capture probabilities using the robust design were small (Dinsmore et al. 2003), we hypothesized that models with constant capture probability would receive better support than those with time-specific capture probability, but this was somewhat speculative. Therefore, we considered the use of both of these constraints on capture probability partly exploratory.

For lambda \((\lambda)\), we considered 4 constraints. We considered 2 models with full time variation where \( \lambda \) varied by year \([\lambda(\cdot)]\); \( \phi \) was also year-specific in both models, while \( p \) was constant in 1 model and year-specific in the other. We also considered a model where \( \lambda \) had a linear time trend \([\lambda(\cdot)]\); \( \phi \) was year-specific, and \( p \) was constant. We next considered a model where \( \lambda \) was constant \([\lambda(\cdot)]\), but only when \( \phi \) and \( p \) were also constant; a model with constant \( \lambda \) and time variation on \( \phi \) and \( p \) was nonsensical. Finally, we considered a model where \( \lambda \) was a function of the hectares of active prairie-dog colonies \([\lambda_{\text{prairie dog}}(\cdot)]\). This latter model was an attempt to solidify the relationship between these 2 species that we found earlier (Dinsmore et al. 2003). Thus, temporal variation in \( \lambda \) was accounted for by recruitment and immigration in the first case and by recruitment, immigration, and apparent survival in the second case. We modeled lambda models on a log scale, where:

\[
\log(\lambda) = \hat{\beta}_0 + \hat{\beta}_1(X),
\]

and \( X \) represented some variable of interest such as the area occupied by prairie dogs or a linear time trend.

In an attempt to better understand possible causes of annual population trends, we also considered a single model where recruitment \((f)\) was estimated instead of population trend \((\lambda)\). In this model, recruitment was a function of the hectares of active prairie-dog colonies and used the same constraints on \( \phi \) and \( p \) that were in the best survival and \( \lambda \) model. Here, \( f \) was defined as the number of new animals in the population at time \( i \) per animal that was in the population at time \( i - 1 \) (Franklin 2000). The relationship between lambda, apparent survival, and recruitment was simply \( \lambda = \phi + f \). Therefore, \( f \) estimated the portion of apparent survival that was due to recruitment. We modeled recruitment models on the log scale, where:

\[
\logit(f) = \ln \left( \frac{f}{1-f} \right) = \beta_0 + \beta_1(X),
\]

and \( X \) represented some variable of interest such as the area occupied by prairie dogs.

With these guidelines, we considered the following 6 models to estimate \( \lambda \) and \( f \):

1. \( \phi(\cdot) p(\cdot) \lambda(\cdot) \)
2. \( \phi(t) p(\cdot) \lambda(\cdot) \)
3. \( \phi(t) p(t) \lambda(t) \)
4. \( \phi(t) p(t) \lambda(t) \)
5. \( \phi(t) p(t) \lambda_{\text{prairie dog}} \)
6. \( f_{\text{prairie dog}}(\cdot) \) with \( \phi \) and \( p \) structure from best \( \lambda \) model

**Goodness-of-fit**

We used the total chi-square value from Tests 2 and 3 in program RELEASE (Burnham et al. 1987) as a test of goodness-of-fit of our mountain plover data to the Pradel lambda model. We checked for overdispersion in these data using an estimate of \( c \) from RELEASE, that we obtained by dividing the total chi-square by its degrees of freedom.

We computed the ratio of differences in log likelihood values as an approximate measure of the proportion of deviance explained by the best model (Skalski et al. 1993). We calculated this quantity as:

\[
\text{Proportion of deviance} = \frac{[\log L (\text{best}) - \log L (\cdot)]}{[\log L (\text{global}) - \log L (\cdot)]}
\]

using log likelihoods from the best model, the global \((\phi(t) p(t) \lambda(t))\) model, and the simplest \((\phi(\cdot) p(\cdot) \lambda(\cdot))\) model. Here, the simplest model had 3 parameters \((\phi, p, \text{and} \lambda)\), and the global model had full year-effects on \( \phi, p, \text{and} \lambda \) (15 parameters).

**Model Selection**

We selected an appropriate model using the methodology of Burnham and Anderson (2002).
First, we ranked the set of $R$ candidate models using Akaike’s Information Criterion (AIC; Akaike 1973). The use of AIC provides a means of objectively ranking a set of models and then selecting a best approximating model or models for inference (Burnham and Anderson 2002). To correct for possible small sample bias, we used AICc to rank models. We defined AICc as:

$$\text{AIC}_c = -2\log L + 2K \left( \frac{n}{n - K - 1} \right)$$

where $\log L$ was the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates, $K$ was the number of estimable parameters, and $n$ was the sample size. Here, the sample size was the total number of releases (new releases plus resightings). The second term in the above equation was a correction for small sample size.

Once we computed AICc values for each model, we ranked the $R$ models relative to the model with the minimum AICc value. We made comparisons between models using AAICc values, where for each model $i$:

$$\text{AAIC}_c = \text{AIC}_c - \text{AIC}_c \text{min}$$

The AAICc values compared the relative distances between the best approximating model ($\text{AIC}_c \text{min}$) and each competing model ($\text{AIC}_c$). Generally, models with $\text{AAIC}_c \leq 2$ have strong support whereas those with $\text{AAIC}_c > 10$ have little support (Burnham and Anderson 2002). We also computed normalized Akaike weights ($w_i$) for each of the $R$ models as:

$$w_i = \frac{e^\left(-\frac{\text{AAIC}_c}{2}\right)}{\sum_{r=1}^{R} e^\left(-\frac{\text{AAIC}_r}{2}\right)}.$$ 

These normalized weights provided another means of directly evaluating the strength of evidence for each model and were useful for computing parameter estimates that reflected model selection uncertainty (Burnham and Anderson 2002). Parameter estimates in MARK were maximum likelihood estimates with 95% confidence intervals based on a logit or log transformation. Instead of using parameter estimates from a single best model, we model averaged (Burnham and Anderson 2002) parameter estimates across all 5 candidate models. This procedure weighted the individual parameter estimates according to their Akaike weights; parameter estimates from models with higher weights received stronger support than those from models with little or no weight.

Using the Akaike weight and estimate of lambda ($\hat{\lambda}$) from each of the $R$ models, we computed a model averaged estimate of $\lambda$ as:

$$\hat{\lambda} = \frac{1}{R} \sum_{r=1}^{R} w_i \hat{\lambda}_i$$

with sampling variance:

$$\text{var}(\hat{\lambda}) = \left[ \sum_{r=1}^{R} w_i \text{var}(\hat{\lambda}_i | M_r) + (\hat{\lambda}_i - \hat{\lambda})^2 \right] \cdot$$

where $M_r$ was the $r$th model in the candidate set (Buckland et al. 1997). The 95% confidence interval for model-averaged estimates of $\lambda$ was:

$$95\% \text{CI}_L = \hat{\lambda}_i - 1.96 \left[ \text{SE}(\hat{\lambda}_i) \right]$$

$$95\% \text{CI}_U = \hat{\lambda}_i + 1.96 \left[ \text{SE}(\hat{\lambda}_i) \right]$$

where:

$$\text{SE}(\hat{\lambda}_i) = \sqrt{\text{var}(\hat{\lambda}_i)}.$$

RESULTS

The pooled results from Tests 2 and 3 in program RELEASE showed there was a good fit to the Pradel lambda model ($\chi^2_{10} = 0.41$). There was no evidence of extra binomial variation in these data ($\hat{\hat{\alpha}} = 1.03$). The proportion of deviance explained by the best model was 49% of variation. Model-averaged estimates of $\lambda$ showed that the population of mountain plovers in southern Phillips County, Montana, increased rapidly from 1995-1998 and then appeared to stabilize in 1999 (Fig. 3). During the period of increase from 1995 to 1998, the estimates of $\lambda$ were $>$1, but $\lambda$ could not reliably be judged different from 1 in 1999.

We found good evidence supporting an effect of the hectares of active prairie-dog colonies on $\lambda$, but the effect on the log scale was negative ($\beta_{\text{prairie-dog}} = -0.11$; 95% CI was $-0.17$, $-0.05$). We also found good evidence for a negative linear time trend in $\lambda$ on the log scale in the third best model ($\beta_T = -0.09$; 95% CI was $-0.14$, $-0.04$). This model had stronger support ($w_i = 0.31$) than models where $\lambda$ was time-specific or constant across time (Table 1).

Using the best lambda and survival model, we estimated recruitment instead of lambda (Table 1). This model received only slightly less support
than the best $\lambda$ model ($\Delta AIC_c = 0.07, w_1 = 0.32$).
The effect of area occupied by prairie dogs was still strongly negative on the logit scale ($\beta_{\text{prairie-dog}} = -0.23; 95\% \text{CI was} -0.36, -0.10$) in this model. Estimates of $f$ gradually declined from 0.72 in 1996 to 0.38 in 2000 (Table 2).

**DISCUSSION**

**Interpretation of $\lambda$**

The model selection results generally agreed with earlier findings on apparent survival and capture probabilities, lending support to estimates of $\lambda$ from the Pradel model. Earlier, we found that adult survival showed little annual variation and that capture probabilities were high with only slight annual variation (Dinsmore et al. 2003). Pradel models with the same constraints on apparent survival and capture probability received the best support of the models we considered. Due to limitations in the Pradel model that forced capture probabilities to be estimated as a single parameter, these estimates of $\lambda$ should still be interpreted with caution. Improper modeling of capture probabilities may have resulted in slightly biased estimates of annual population trends. Ultimately, a robust design Pradel model is needed to properly model capture probabilities and generate less biased estimates of $\lambda$ for this population.

Estimates of $\lambda$ are susceptible to bias if the size of the study area changed during the study (Franklin et al. 1999). In our study, population trends represented real trends and were not a reflection of changes in the size of area studied. The boundaries of the study area were fixed for the duration of the 6-year study. Within the study area, we attempted to survey all known prairie-dog colonies for plovers. We occasionally missed some small colonies, but plovers seldom occupied these colonies (Olson-Edge and Edge 1987). Thus, study area coverage was nearly complete each year, and population trends reflected real changes in the numbers of mountain plovers within this area.

**Prognosis**

At present, the mountain plover population in southern Phillips County appears to be stable at approximately 175 individuals (Dinsmore et al. 2003). The viability of such a small population is unknown, although they successfully rebounded from estimated population levels below 100 individuals in the mid-1990s. Our results suggest that the population increased rapidly from 1995 to 1998, possibly from in situ reproduction, but more likely from a combination of reproduction and...
immigration from surrounding areas such as Fort Belknap Indian Reservation (Dinsmore et al. 2003). During 2000–2001, there were signs of another sylvatic plague outbreak in prairie dog populations in southern Phillips County. Because mountain plovers in this region are closely tied to black-tailed prairie dog numbers, any future reductions in area occupied by prairie dogs will likely negatively impact plovers. Monitoring plovers through a sylvatic plague outbreak would be useful for noting the timing and magnitude of declines and recovery and correlating these changes to the area occupied by prairie dogs.

We cannot address whether the estimate of 175 breeding adults is sufficient to sustain this population for an extended period. Recruitment was high in 1995, but it gradually declined with an increase in the area occupied by prairie dogs, a pattern similar to that exhibited by estimates of annual survival (Table 2). The high estimates of recruitment relative to estimates of survival suggest that recruitment was an important component of population growth in this population. This in turn suggests that immigration may have played an important role in this rapid recovery.

We found a strong negative relationship between the area occupied by prairie dogs and both λ and \( f \). Prairie-dog colonies were a preferred habitat for mountain plovers in this region (Olson 1984), so we initially expected to find a positive relationship between area occupied by prairie dogs and both population growth and recruitment. It is clear that this population is rebounding in concert with an increase in the area occupied by prairie dogs. If the rate of change in the area occupied by prairie dogs was slower than the rate of change in plover numbers, then such a negative relationship could result. The result was that plovers may not have been able to colonize new prairie dog colonies as fast as they were becoming available. Or, perhaps the area occupied by prairie dogs was not the best measure of plover habitat; colony-specific features, the spatial arrangement of colonies, or the site fidelity of plovers may all be more important, and these factors are not related to the total area occupied by prairie dogs.

This information should provide a more solid foundation on which to build conservation measures for mountain plovers. Mountain plovers were recently identified as highly imperiled in a review of North American shorebirds, 1 of 5 shorebird species receiving this designation (Brown et al. 2001). A petition to federally list the species as Threatened was withdrawn in 2003 (U.S. Depart-


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