RESEARCH ARTICLE

Apparent survival of adult Burrowing Owls that breed in Canada is influenced by weather during migration and on their wintering grounds

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ABSTRACT

Understanding factors that influence the survival of endangered migratory species is critical for making informed management decisions, yet this understanding relies on long-term recapture datasets for species that are, by definition, rare. Using 3 geographically widespread (Saskatchewan, Alberta, and Manitoba, Canada) and long-term (6–15 yr) mark–recapture datasets, we quantified spatial and temporal variation in apparent annual survival and recapture probabilities of Burrowing Owl (*Athene cunicularia*), an endangered species that breeds in Canada. We then examined how large-scale weather patterns during migration (storms) and on the wintering and breeding grounds (precipitation), in addition to prey irruptions on the breeding grounds, influenced apparent survival of Burrowing Owls. Female Burrowing Owls had lower apparent survival than males in all 3 study areas. Storms during fall migration and above-average precipitation on the wintering grounds were associated with reduced apparent survival of Burrowing Owls in the longest-running study area, Saskatchewan; in Alberta and Manitoba, there were few correlations between apparent survival of Burrowing Owls and weather or prey irruptions. Increases in stochastic events such as storms during migration or precipitation on the wintering grounds could have adverse consequences on the already small Burrowing Owl population in Canada. Local management actions that focus solely on improving adult apparent survival within Canada are likely insufficient for mitigating susceptibility of adults to inclement weather or other factors outside the breeding season, underscoring the need for management of this species across multiple jurisdictions within North America.

Keywords: apparent survival, *Athene cunicularia*, breeding grounds, migration, prey abundance, Program MARK, storms, wintering grounds

Supervivencia aparente de *Athene canicularia* reproduciéndose en Canadá es afectada por condiciones meteorológicas durante su migración y en su área de invernada

RESUMEN

Un conocimiento de los factores que influyen en la supervivencia de especies migratorias en peligro de extinción es crítico para las decisiones de manejo, pero este conocimiento depende de la disponibilidad de datos de recaptura colectados a largo plazo para especies que son, por definición, raras. Usando tres conjuntos de datos de marcado y recaptura con amplia representación geográfica (Saskatchewan, Alberta, y Manitoba, Canadá) y recolectados a largo plazo (6–15 años), cuantificamos la variación espacial y temporal en supervivencia aparente anual y en probabilidades de recaptura para *Athene canicularia*, una especie en peligro de extinción que se reproduce en Canadá. Luego examinamos como patrones de condiciones meteorológicas a gran escala durante la migración (tormentas) y en áreas de invernada y reproducción (precipitación), tanto como irrupciones de presas en las áreas de reproducción, afectan la supervivencia aparente de *A. canicularia*. Las hembras de *A. canicularia* tuvieron una supervivencia aparente inferior a la de los machos en las tres áreas de estudio. Tormentas durante la migración de otoño, y precipitación superior al promedio en las áreas de invernada, fueron asociadas con una supervivencia aparente reducida en los búhos del área de estudio con el seguimiento más prolongado, Saskatchewan; en Alberta y Manitoba, hubo pocas correlaciones entre supervivencia aparente de búhos y condiciones meteorológicas o irrupciones de presas. Aumentos en eventos estocásticos como tormentas durante la migración o precipitación en áreas de invernada podrían afectar

negativamente las poblaciones ya reducidas de *A. canicularia* en Canadá. Acciones de manejo local que se enfocan solamente en mejorar la supervivencia aparente de adultos dentro de Canadá probablemente serán insuficientes para mitigar la susceptabilidad de adultos al mal tiempo, u otros factores, fuera de la época reproductiva, justificando la necesidad de manejar esta especie a lo largo de múltiples jurisdicciones dentro de norteamérica.

Palabras clave: abundancia de presas, áreas de invernada, áreas de reproducción, *Athene canicularia*, migración, programa MARK, supervivencia aparente, tormentas

INTRODUCTION

Survival is a fundamental component of individual fitness and a key vital rate needed for estimating population change for endangered species management (Boyce 1992). Deriving annual survival estimates for endangered species is challenging because of their small population sizes and the need for long-term (>3 yr) mark–recapture data (Beissinger and Westphal 1998). Information on factors influencing adult survival can help determine whether conservation initiatives should target adult survival to influence population persistence or whether management focused on other demographic parameters could be more influential. For migratory endangered species in particular, the above information can also help geographically target management activities to the most appropriate stage(s) of the species' annual cycle: migration, breeding, or wintering (Martin et al. 2007, Franke et al. 2011).

Weather can influence apparent survival probabilities for species during the breeding and nonbreeding seasons (Stokke et al. 2005, Salewski et al. 2013). Inclement weather on the breeding grounds may also reduce breeding success (Steenhof et al. 1997, Wellicome 2000), thereby increasing subsequent breeding dispersal (Catlin and Rosenberg 2006)—which, in turn, can reduce estimated apparent survival. The majority of research linking winter weather (e.g., storm events, precipitation, and temperature) and climate (e.g., El Niño–Southern Oscillation, Pacific Decadel Oscillation) to annual survival has been conducted on nonmigratory birds (e.g., Northern Spotted Owl [*Strix occidentalis caurina*]; Seamans et al. 2002, Glenn et al. 2011), but evidence is accumulating that weather on the wintering grounds also influences annual survival in migratory species (Sillett et al. 2000, Nevoux et al. 2007, Macías-Duarte and Panjabi 2013). The influence that weather conditions during migration have on adult apparent survival is not well established (but see Franke et al. 2011, Klaassen et al. 2014), despite evidence that storms contribute to mass avian mortality (Newton 2006, 2007) or cause individuals to be pushed off course so that they breed elsewhere (Lens 1995). Lastly, inclement weather during the breeding season can have carryover effects (Norris 2005) in other periods within the annual cycle by increasing migratory and overwinter mortality (Hakkarainen et al. 2002).

The abundance of prey on the breeding grounds is another potentially important influence on adult survival. For example, overwinter survival in some owl species is higher in years following breeding-season prey irruptions than following low-prey years (Great Horned Owl [*Bubo virginianus*], Houston and Francis 1995; Ural Owl [*Strix uralensis*], Brommer et al. 2002; Boreal Owl [*Aegolius funereus*], Hakkarainen et al. 2002). The consumption of abundant prey likely improves body condition and energy reserves of predatory birds, which may allow them to better withstand migration or overwinter conditions (Hakkarainen et al. 2002). Unfortunately, the fluctuating nature of most prey of predatory birds requires long-term mark–recapture datasets to capture the wide variation in annual apparent survival that may result from irruptive prey. We are unaware of any previous studies that have examined how factors during breeding, wintering, and migration may influence apparent adult survival of a migratory owl in North America.

Burrowing Owls (*Athene cunicularia*) are considered endangered in Canada (COSEWIC 2006), subject to special protection in Mexico (SEMARNAT 2010) and a species of conservation concern in the United States (Klute et al. 2003). In the past 3 decades, the Canadian population of Burrowing Owls has declined by $>90\%$ and their range has contracted by $\geq65\%$ (COSEWIC 2006). Adult survival in resident Burrowing Owl populations can, under certain conditions, have an important influence on population growth rate (Gervais et al. 2006), yet it is uncertain if high emigration or low adult Burrowing Owl survival explain the population declines observed in prairie Canada, where these owls are invariably migratory. An understanding of factors that influence variation in Burrowing Owl apparent survival is a major knowledge gap identified in the Recovery Strategy for the Burrowing Owl in Canada (Environment Canada 2012). Determining where (wintering, breeding, or migration route) and at what stage (adult survival, juvenile survival, or productivity) demographic "bottlenecks" occur in Burrowing Owls is important for prioritizing and targeting management activities (Environment Canada 2012).

Using geographically widespread (1 study area in each of the 3 provinces in the Canadian prairies, covering $>27,000$ km^2) and long-term (6–15 yr) mark–recapture datasets, our primary objective was to quantify spatial and temporal

variation in apparent survival and recapture probabilities of migratory Burrowing Owls breeding in prairie Canada. Our secondary objective was to test the hypothesis that environmental conditions across the annual migratory cycle influence survival by relating patterns of annual apparent survival to large-scale indices of weather on the breeding and wintering grounds, storm events on the Burrowing Owls' migration route, and prey irruptions on the breeding grounds. Storms during spring and fall migration could affect apparent survival estimates by directly increasing mortality or by changing the relative benefit of continuing migration such that Burrowing Owls stop migration and breed elsewhere. Mark–recapture data, such as ours, cannot discriminate between these 2 scenarios because death cannot be separated from permanent emigration (survival is biased low when emigration is high). Under either scenario, however, we predicted there would be a negative relationship between the number of storms and apparent survival. Similarly, we also predicted that above-average precipitation on the breeding grounds would adversely affect reproductive success or body condition, causing Burrowing Owls to permanently emigrate from the breeding site for subsequent breeding seasons or else suffer increased overwinter mortality. We predicted that prey (grasshopper [Orthoptera: Acrididae] and vole [*Microtus pennsylvanicus*]) irruptions on the breeding grounds would lead to increased adult apparent survival in the interval following the breeding season. Deviation of precipitation from normal conditions on the wintering grounds could have either a positive or a negative effect on Burrowing Owl apparent survival through influences on prey populations or vegetative cover.

METHODS

Study Sites

We studied Burrowing Owls across their breeding range in prairie Canada by establishing study areas in Alberta (AB: 1986–1997), Saskatchewan (SK: 1988–2003), and Manitoba (MB: 1989–1994) (Figure 1). The owls occupied sites, within the Grassland Ecoregion, that were dominated by rangeland grazing and dryland crop production (Clayton and Schmutz 1999, Poulin et al. 2005). They typically arrived in Alberta and Saskatchewan in late March or early April and began nesting in early May (Wellicome 2000), with arrival and nesting in Manitoba occurring ~2 wk later (K. De Smet personal observation). The nesting cycle lasted ~12 wk, and the owls departed on fall migration between September and October (Poulin et al. 2011). Burrowing Owls that breed in Canada migrate through the Great Plains and overwinter in southern Texas and central Mexico (James 1992, Duxbury 2004, Holroyd et al. 2010, Poulin et al. 2011).
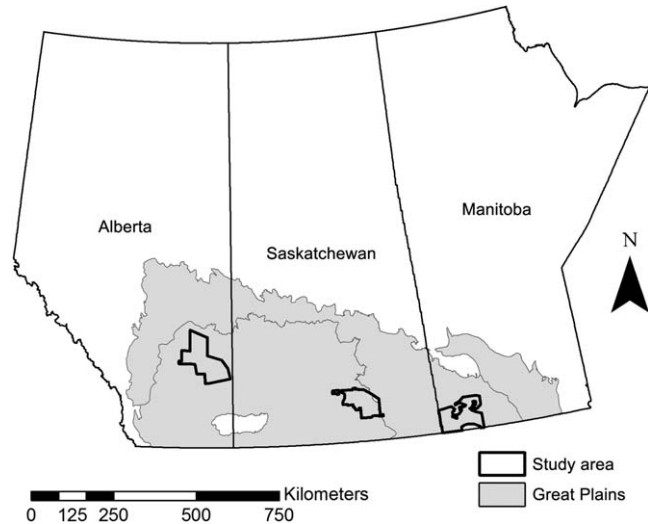

FIGURE 1. Location of study sites in Alberta (area = 11,285 km^2), Saskatchewan (6,926 km^2), and Manitoba (8,807 km^2), Canada, where Burrowing Owls were banded.

Field Methods

Each year, we surveyed parcels of land in each study site that had been occupied by Burrowing Owls in previous years, where suitable habitat (grazed pastures with abundant ground squirrels) existed near former breeding sites, or where Burrowing Owls had been reported by landowners, the general public, regional biologists, and environmental consultants. Sampling efforts within a study area were consistent among years but differed among study areas. We captured adults from May to August and determined the sex of each individual by the presence or absence of a well-developed brood patch. Captured adults were banded with a numbered aluminum leg band and sometimes a unique set of colored leg bands; nestlings were banded with a numbered aluminum leg band each year in June and July. All individuals had to be captured and banded or resighted at an active burrow; therefore, no transients could be included. Adults returning to the study areas were identified either by their unique aluminum and color-band combination when they were resighted or by their uniquely numbered aluminum band when recaptured. We did not examine first-year survival because of the very low return probabilities of juveniles (Wellicome et al. 2013). However, if a bird banded as a nestling returned to the study area and was identified or captured at an active nest, it was subsequently included in the analyses examining adult apparent survival for the following year.

Apparent Survival Covariates

Breeding grounds. We included an index of summer precipitation (June–August) calculated by using ClimateWNA version 4.72 (Wang et al. 2012). ClimateWNA
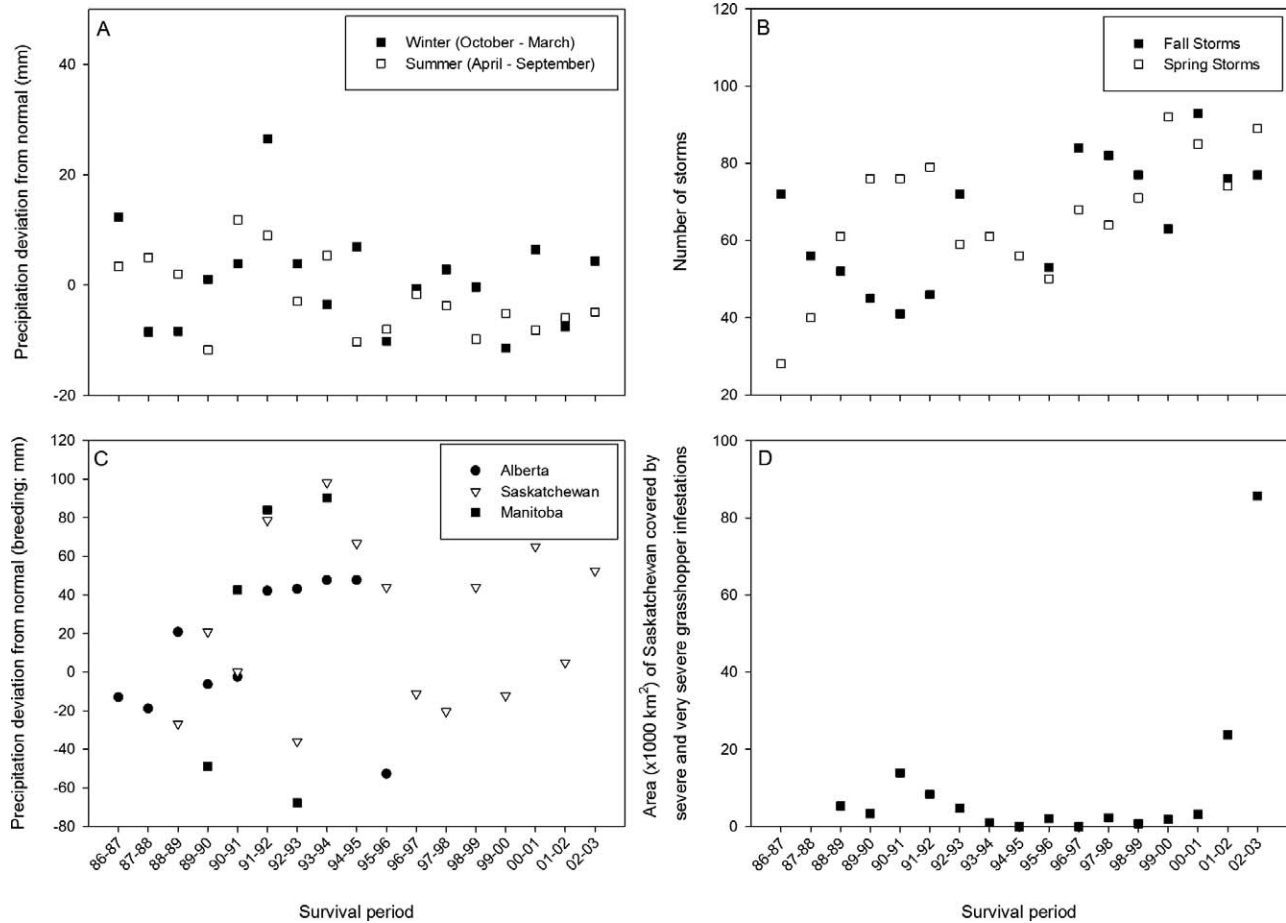
FIGURE 2. Yearly values for (**A**) winter (October–March) and summer (April–September) precipitation deviations from normal conditions on Burrowing Owl wintering grounds; (**B**) numbers of fall (September–October) and spring (March–April) storm events (tornadoes, hail, and thunderstorm winds) during migration; (**C**) breeding-season (June–August) precipitation deviation from normal; and (**D**) estimates of the area of Saskatchewan, Canada, covered by severe (12–24 grasshoppers m^{-2}) and very severe (>24 grasshoppers m^{-2}) grasshopper outbreaks.

provides a user-friendly interface for accessing historical climate information in Canada for point estimates based on latitude, longitude, and elevation (Wang et al. 2012). We constructed a regularly spaced 1×1 km grid across each study area and, for each point, calculated summer precipitation totals (mm) for each study year and historical normal summer precipitation (mm; 1961–1990). We then calculated the yearly deviation from normal (mm) for each point (yearly summer precipitation − normal summer precipitation). Our index of deviation from normal summer precipitation (BreedingPrecip) was then the average deviation from normal across all grid points in each study area (Figure 2).

We included abundance of voles (Voles) and grasshoppers (Grasshoppers) on the breeding grounds as 2 potential factors influencing Burrowing Owl apparent survival. In 1997, we observed an unusually high average number of voles in Burrowing Owl prey caches (30 voles

cache^{-1}), which suggested that a vole irruption had occurred in SK (Poulin et al. 2001, Wellicome 2005). Burrowing Owl average prey caches in all other years contained <10 voles (Poulin et al. 2001). For SK, we used a binary variable (1 = irruption year [1997], 0 = normal year) and assumed that the vole irruption in 1997 influenced apparent survival for the 1997–1998 period. Because we did not have information on vole irruptions in the AB study area per se, we used an unpublished dataset that recorded the number of voles in Swainson's Hawk (*Buteo swainsoni*) nests in roughly the same area as the Burrowing Owl study area (Schmutz et al. 2006). We standardized our index of vole abundance by calculating the average number of voles observed in a Swainson's Hawk nest per nest visit per year (J. K. Schmutz personal observation). Suitable data on vole abundance were not available in MB.

Grasshoppers (Orthoptera) can be an especially important part of the adult diet when they are feeding nestlings

during the breeding season (Schmutz et al. 1991, Poulin et al. 2011). Data on grasshopper abundance relevant to the years of our study were available only for SK. We used grasshopper survey maps from 1988–2003 (Olfert et al. 2006) and summed the area of SK (km^2) covered by severe (12–24 grasshoppers m^{-2}) and very severe (>24 grasshoppers m^{-2}) grasshopper infestations for use as an explanatory variable (Figure 2). Unfortunately, these survey maps were not available in GIS format but still encompassed the SK distribution of breeding Burrowing Owls; however, they included information for northern extremes (aspen parkland and moist–mixed grassland regions) of the traditional breeding distribution of Burrowing Owls (Olfert et al. 2006).

Wintering grounds. We also included an index of wet or dry monthly conditions on the Burrowing Owl wintering grounds as a potential explanatory variable. We used the World Climate Research Programme and Global Climate Observing System's gauge-based monthly world precipitation map (0.5° × 0.5° grid; http://iridl.ldeo.columbia.edu/SOURCES/.WCRP/.GCOS/.GPCC/). We limited our analysis to an area bounded by 30°N to 20°N and 117°W to 94°W (southern Texas to central and northern Mexico, the approximate wintering grounds of Canadian Burrowing Owls; Holroyd et al. 2010). We used the European Space Agency's GlobCover Land Cover 2009 (ESA GlobCover Project, MEDIAS-France) GIS layer to further limit our analysis to grid-cell centers that overlapped suitable Burrowing Owl habitat (cropland, grassland, and sparse vegetation landcover types). We calculated the average monthly deviation (mm) from normal precipitation (average precipitation, for the 1951–2000 period, for each grid-cell and month combination) for the periods of October–March (PrecipWinter) and April–September (PrecipSummer) in an area. Negative values indicate lower-than-normal precipitation, and positive values indicate higher-than-normal precipitation for each period (winter or summer) within this area (Figure 2).

Small mammals can show a delayed numerical response to rainfall of ≥1 yr (e.g., Jaksic et al. 1997, Thibault et al. 2010), and grass height and density during the months when Burrowing Owls are on their wintering grounds may also be influenced by precipitation in the previous winter (Macías-Duarte and Panjabi 2013). Therefore, we also included an effect of winter precipitation from the year preceding the apparent survival estimate of interest (PrecipWinter1YrLag; e.g., we used precipitation from the winter of 1995–1996 to explain variation in Burrowing Owl apparent survival between 1996 and 1997; Figure 2).

Migration. Burrowing Owls nesting in Canada most likely migrate through Montana, North Dakota, South Dakota, Wyoming, Colorado, Nebraska, Kansas, New Mexico, Texas, and Oklahoma (Holroyd et al. 2010) during

the periods of September–October (Todd et al. 2003) and March–April. We accessed information from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/dataaccesstools.html#climate) on the number of storm events (tornados, hail, and thunderstorm winds) in these 10 states during September–October (FallStorms) and March–April (SpringStorms). Tornados, hail, and thunderstorms occurring on the same day within the same state were considered to be 1 storm event. We then calculated the total number of storm events per period (fall or spring) per year within the 10 states. The number of storm events has increased in recent years (Figure 2) because of increased reporting probabilities; however, other studies have documented a "persistent minimum [number of tornados] in the late 1980s" and a subsequent increased number of storms in the 1990s and 2000s even after accounting for reporting rate (Karl et al. 2008:76).

Statistical Analyses

We used a Cormack-Jolly-Seber capture–recapture model in Program MARK version 7.1 to determine apparent survival (Φ) and recapture probability (p) of adult Burrowing Owls for each study area (White and Burnham 1999). We analyzed each study area separately because recapture effort differed among study sites, the years that each study site were active did not overlap, and not all covariates were available in each study area. Owl banding and resighting did not occur in AB in 1994, so we adjusted the recapture interval length to 2 yr between 1993 and 1995 (covariates were averaged for 1993 and 1994 or for 1994 and 1995, depending on the covariate of interest); otherwise, the interval between recaptures was always 1 yr for all study areas.

To ensure that our data met the assumptions of mark–recapture analysis, we examined the variance inflation factor ($\hat{c}$) using the deviance procedure (White and Burnham 1999). We derived $\hat{c}$ from running the bootstrap goodness-of-fit procedure using 100 simulations for the most parameterized model without covariates (White and Burnham 1999). A $\hat{c}$ value of 1 indicates perfect fit of the model to the data, whereas a $\hat{c}$ between 1 and 4 represents acceptable model fit (Burnham and Anderson 1998). For all of our analyses, $\hat{c}$ ranged from 1.1 to 1.5, so we adjusted $\hat{c}$ accordingly and used quasi–Akaike's Information Criterion adjusted for small sample sizes (QAIC$_c$) for model selection.

Recapture probability. We included the effects of sex on recapture probability in all analyses because males may be more easily resighted than females during the breeding season. However, we also examined recapture models that included year (t) or a linear time trend (T), as well as all possible two-way interactions with sex (Table 1). We used the top p model, as supported by QAIC$_c$, in all further

TABLE 1. Development of the candidate list of models explaining variation in apparent survival (Φ) and recapture (p) probabilities of Burrowing Owls in Saskatchewan (SK; 1988–2003), Alberta (AB; 1986–1996), and Manitoba (MB; 1989–1994), Canada. We used explanatory variables that best explained p before examining the variables that best described Φ. Explanatory variables include sex, time (t), linear time trend (T), deviations from normal precipitation from April–September (PrecipSummer) and October–March (PrecipWinter) on the wintering ground, and a 1-yr lag in the winter precipitation parameter (PrecipWinter1YrLag), winter precipitation parameter (PrecipWinter1YrLag), deviation from normal precipitation on the breeding grounds in summer (BreedingPrecip), the number of storm events during spring (SpringStorms) and fall (FallStorms) migration, and the abundance of voles (Voles) and grasshoppers (Grasshoppers) on the breeding ground. We examined both linear (L) and quadratic (Q) changes in Burrowing Owl apparent survival in relation to several variables of interest. The "Study areas" column lists the study areas for which the model was examined.

Model set		Φ	Relationship examined	p	Study areas
p		Φ(sex + t + sex*t)			
				p(sex)	AB,SK, MB
				p(sex + t)	AB,SK, MB
				p(sex + T)	AB,SK, MB
				p(sex + t + sex*t)	AB, SK, MB
				p(sex + T + sex*T)	AB,SK,MB
Φ					
	Wintering	Φ(sex + PrecipSummer)	L,Q	p(sex or top model from above)	AB,SK, MB
		Φ(sex + PrecipWinter)	L,Q	p(sex or top model from above)	AB,SK, MB
		Φ(sex + PrecipWinter1YrLag)	L,Q	p(sex or top model from above)	AB,SK, MB
	Migration	Φ(sex + FallStorms)	L	p(sex or top model from above)	AB,SK, MB
		Φ(sex + SpringStorms)	L	p(sex or top model from above)	AB,SK, MB
		Φ(sex + FallStorms + SpringStorms)	L	p(sex or top model from above)	AB,SK, MB
	Breeding	Φ(sex + Voles)	L	p(sex or top model from above)	AB, SK
		Φ(sex + Grasshoppers)	L	p(sex or top model from above)	SK
		Φ(sex + Voles + Grasshoppers)	L	p(sex or top model from above)	SK
		Φ(sex + BreedingPrecip)	L,Q	p(sex or sex or top model from above)	AB, SK, MB

analyses examining the relationships between our covariates and apparent survival.

Apparent survival. Sex was included in all models because we expected differences in apparent survival between males and females. Using QAIC$_c$, we first examined whether apparent survival varied either linearly or nonlinearly (quadratic relationship) in response to all wintering- and breeding-ground weather-related variables. All quadratic models relating apparent survival to breeding- and wintering-ground precipitation were >2 ΔQAIC$_c$ units from linear models, so we retained the linear models for further analyses. We predicted that apparent survival of adult Burrowing Owls would increase with increasing prey abundance on the breeding grounds and decrease with an increasing number of storm events during migration, so we considered only linear changes in apparent survival in response to these covariates. Explanatory variables were not highly correlated (all $r < 0.5$), so all were included in the analyses. To determine whether additional variation in adult apparent survival could be explained by wintering-ground, migration-route, or breeding-ground covariates, we separately added these variables to the apparent survival model with sex effects (Table 1). Breeding-ground, migration-route, or wintering-ground models that outperformed the sex-only model (i.e. models with the parameters of interest had a lower QAIC$_c$ in relation to the sex-only model; Table 1) were combined into 1 global model. We

then examined all possible subsets of this global model and used QAIC$_c$ to rank models. We based our inferences on whether model-averaged (if necessary; see results) parameter estimates of variables included in the top models (ΔQAIC$_c$ < 2.0) had 85% confidence intervals (CIs) that did not include zero (Arnold 2010). Basing inferences on variables within 85% CIs that did not overlap zero is slightly liberal (i.e. it may include variables with weak effects); however, to remain AIC compatible, Arnold (2010) recommended retaining variables in top models with 85% CIs that do not include zero.

We also conducted a separate analysis in which we pooled data from all study sites when Burrowing Owls were being actively marked and recaptured (1989–1993). Study site and sex were included in all Φ and p models. To reduce model complexity due to small sample sizes and a reduced number of years, we did not test whether there were yearly differences or linear trends in recapture probability. We examined the effects of WinterPrecip, PrecipWinter1YrLag, or SummerPrecip (whichever had the lowest QIAC$_c$) and of BreedingPrecip, FallStorms, and SpringStorms on Φ. Again, to reduce model complexity, we did not include all covariates of interest in 1 global model; rather, we simply examined each in a univariate manner and present a relative comparison of the effects of each. Although there were several female Burrowing Owls captured and recaptured in Alberta

during this period, there was only 1 that was not recaptured in consecutive years, so p was fixed at 1 for females in Alberta.

RESULTS

We banded 332 males and 407 females in SK, 174 males and 195 females in AB, and 76 males and 68 females in MB. We recorded 196 resightings in SK (range: 4–23 yr^{-1}), 47 in AB (range: 1–9 yr^{-1}), and 47 in MB (range: 5–13 yr^{-1}). Apparent survival was ~15% lower for females than for males in each of the 3 provincial study areas (Figure 3A). Burrowing Owl apparent survival in AB was ~20% lower than apparent survival in either SK or MB (Figure 3A). Recapture probabilities were constant across all years in MB and AB; but in SK, recapture probabilities increased over the period of study (Figure 3B).

Reduced apparent survival of Burrowing Owls in SK was related to an increased number of storms during fall and during spring migration, although the 85% CIs of spring migration included zero (Tables 2 and 3; Figure 4). Apparent survival in SK decreased in response to a 1-yr lag effect of winter precipitation on the wintering grounds (Tables 2 and 3; Figure 4). Grasshopper abundance on the breeding grounds explained little variation in Burrowing Owl apparent survival in SK (Table 2). Vole abundance also explained little variation in Burrowing Owl apparent survival in AB and SK (Table 2). In AB, apparent survival decreased as PrecipWinter increased, but this model was within 2 $\Delta QAIC_c$ of the constant-only model, which suggests that the effect of PrecipWinter was relatively weak (Tables 2 and 3; Figure 4). We did not model-average the parameter estimate of PrecipWinter because it was the only model that had a $QAIC_c$ lower than the sex-only model (Table 2). Compared to the sex-only model, none of the explanatory variables explained additional variation in Burrowing Owl apparent survival in MB (Table 2). Neither summer precipitation on the wintering grounds nor breeding-season precipitation on the breeding grounds had an effect on apparent survival in any study site (all $\Delta QAIC_c \geq 2$).

When studies were simultaneously active in all 3 study areas (1989–1993), the top model included only study-site and sex effects on Φ and p (Table 4), and the 85% CIs of all covariates of interest (WinterPrecip1YrLag, FallStorms, SpringStorms, and BreedingPrecip) included zero, even though they were within 2 $\Delta QAIC_c$ of the top model. Average ($\pm$ SE) apparent survival during this period, across all study areas, was 0.44 $\pm$ 0.05 for males and 0.21 $\pm$ 0.03 for females.

DISCUSSION

We found evidence that conditions outside of the breeding season influenced annual apparent survival of migratory
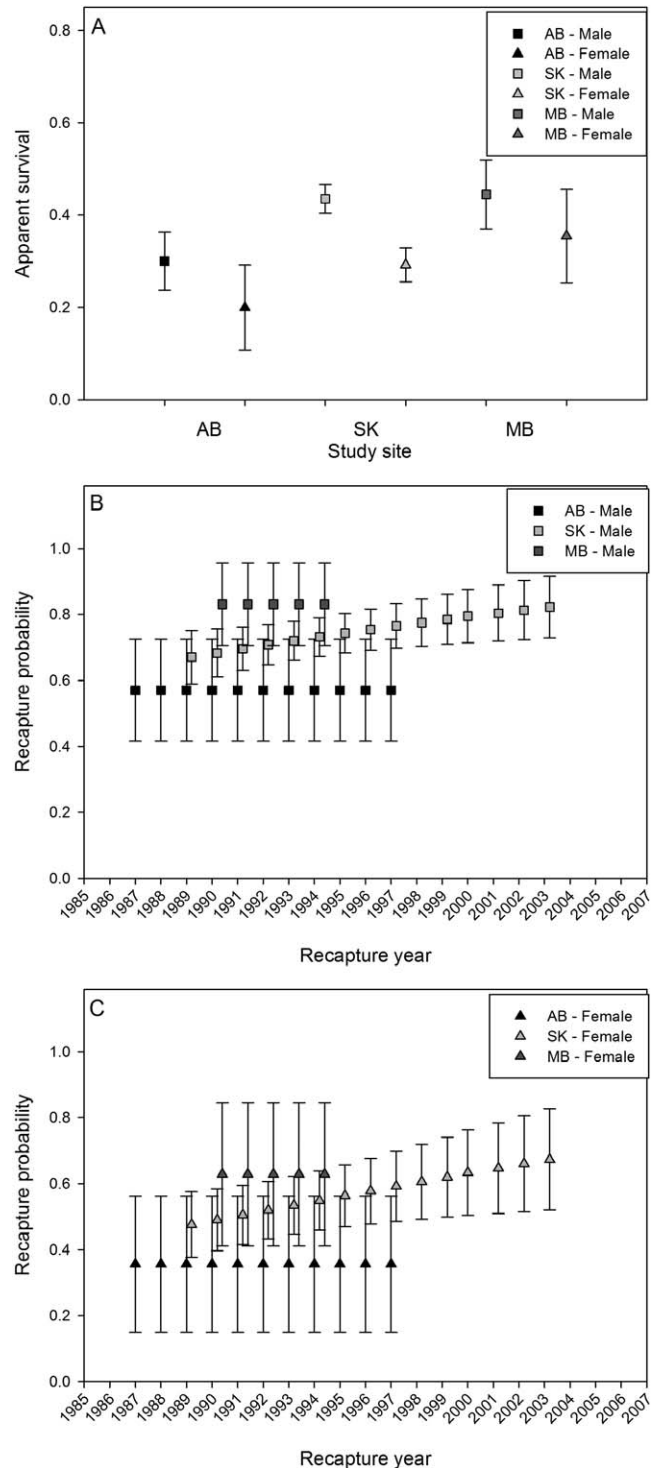
FIGURE 3. Annual apparent survival (**A**) and recapture probabilities of male (**B**) and female (**C**) Burrowing Owls in Saskatchewan (SK; 1988–2003), Manitoba (MB; 1989–1994), and Alberta (AB; 1986–1997), Canada, based on models of annual apparent survival and recapture for each study area (i.e. sex differences in Φ in all 3 study areas and sex differences in p in AB and MB, and a linear time trend and sex differences in p in SK). Results are presented $\pm$ SE.

TABLE 2. Top models explaining variation in annual apparent survival (Φ) and recapture (p) probabilities of Burrowing Owls in Saskatchewan (SK; 1988–2003), Alberta (AB; 1986–1996), and Manitoba (MB; 1989–1994), Canada. Model parameters are the same as in Table 1. Models presented are those within 2 $\Delta QAIC_c$ units of the top model; also included are the base Φ and p models for comparison.

Study site	Model	$\Delta QAIC_c$	w_i	K
AB	Φ(sex [a] + PrecipWinter [a]) p(sex)	0.00 [b]	0.29	5
	Φ(sex) p(sex)	1.19	0.16	4
SK	Φ(sex [a] + FallStorms [a] + SpringStorms + PrecipWinter1YrLag [a]) p(sex + T)	0.00 [c]	0.24	8
	Φ(sex + FallStorms + PrecipWinter1YrLag) p(sex + T)	0.09	0.23	7
	Φ(sex + FallStorms) p(sex + T)	0.45	0.19	6
	Φ(sex + FallStorms + SpringStorms) p(sex + T)	1.79	0.10	7
	Φ(sex) p(sex + T)	3.86	0.04	5
MB	Φ(sex [a]) p(sex)	0.00 [d]	0.44	4
	Φ(sex + PrecipWinter) p(sex)	1.64	0.19	5

[a] Variables in top models ($\Delta QAIC_c = 0$) whose parameter estimates had 85% confidence intervals (model-averaged in SK; not model-averaged in AB and MB) that did not include zero.
[b] $QAIC_c = 241.97$.
[c] $QAIC_c = 899.68$.
[d] $QAIC_c = 154.47$.

Burrowing Owls, more so than factors on the breeding ground. Higher precipitation on the wintering grounds during the wintering season and a larger number of storms experienced during migration were each associated with lower apparent survival of this endangered species. By contrast, there was no evidence that prey abundance or precipitation on the breeding grounds influenced annual apparent survival. These patterns were most obvious in the longest-running study area (SK), likely because of the larger sample size and larger range of values of explanatory variables. We also found that female apparent survival was consistently lower than male apparent survival in each of the 3 study areas.

Apparent Survival of Males and Females

Female apparent survival was ~15% lower than that of males in each of the 3 study areas. Annual survival of nonmigratory Burrowing Owls was 7% higher in males than in females in Florida (Millsap 2002) and 10–20% higher in males than in females in a partially migratory

TABLE 3. Parameter estimates (β), SE, and 85% confidence intervals (CI) for parameters explaining Burrowing Owl apparent survival (Φ) in the top model for Alberta (AB) and model-averaged for Saskatchewan (SK). No covariates were included in the top model in Manitoba, so MB is not presented here. Model parameters are the same as in Table 1.

	β	SE	85% CI
SK: top model (Sex + FallStorms + SpringStorms + PrecipWinter1YrLag)			
FallStorms	−0.015	0.006	−0.024 to −0.006
SpringStorms	−0.013	0.009	−0.026 to −0.0001
PrecipWinter1YrLag	−0.018	0.013	−0.037 to −0.005
AB: top model (Sex + WinterPrecip)			
WinterPrecip	−0.031	0.018	−0.057 to −0.005

population in Washington (Conway et al. 2006). However, Lutz and Plumpton (1997) found that male and female Burrowing Owls, in a migratory population in Colorado, had similar apparent survival probabilities (0.37, both sexes combined). Several hypotheses, which are not mutually exclusive, exist to explain why apparent survival may differ between males and females. There appears to be little energetic constraint during egg laying and incubation in female Burrowing Owls (Wellicome 2005, Wellicome et al. 2013), which suggests that higher energetic investment during reproduction would be an unlikely explanation for lower apparent survival in females than in males. Several non mutually exclusive hypotheses exist for why apparent survival may differ between males and females. Alternately, if males are dominant, females may be displaced from high-quality to low-quality habitat (Marra et al. 1998) and, therefore, suffer higher overwinter mortality. Last, because capture–recapture models are unable to separate permanent emigration from mortality (Lebreton et al. 1992), it is possible that the lower apparent survival of female Burrowing Owls results from lower site fidelity and tendency to disperse farther (Wellicome et al. 1997, Catlin 2004, Duxbury 2004). Regardless, it is of concern that female apparent survival is <0.40 in all study areas and as low as 0.16 in AB. Low female fidelity to breeding locations in Canada could limit the number of nests initiated each year.

Cost of Migration

Migration is energetically costly and can be reflected in reduced overwinter survival probabilities in migratory compared with resident populations (Kaitala et al. 1993). Our estimates of apparent survival for migratory adult Canadian Burrowing Owls (0.16–0.46) are similar to an
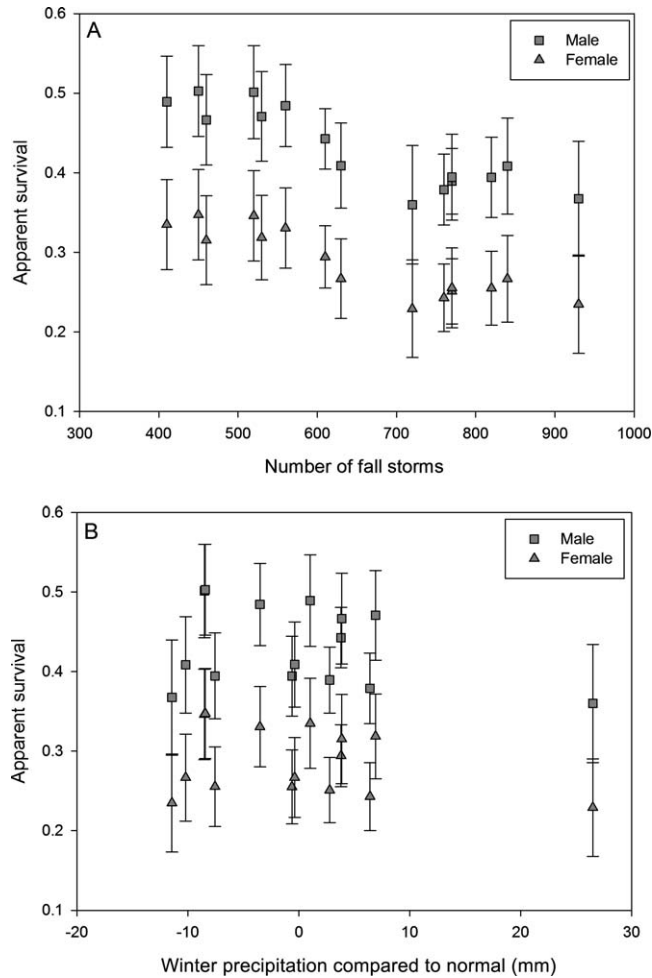
FIGURE 4. Model-averaged yearly apparent survival probability (± SE) of male and female Burrowing Owls in Saskatchewan, Canada, in relation to (**A**) the number of fall (September–October) storm events and (**B**) a 1-yr lag effect of winter precipitation compared to normal on the wintering grounds.

average estimate of apparent annual survival for a migratory population in Colorado (0.37; Lutz and Plumpton 1997). These values are in contrast to higher survival estimates for resident Burrowing Owls in California (0.81, Thomsen 1971; 0.29–0.58, Gervais et al. 2006) and Florida (0.64–0.71, Millsap 2002), indicating that there could be

substantial mortality during migration or significant permanent emigration from study areas by migratory individuals. The relationship between apparent survival and both spring and fall storm events and apparent survival is consistently negative in all our analyses, which suggests that storms during migration may play an important role in the population viability of Canadian Burrowing Owls.

Ideally, following migrating Burrowing Owls using satellite transmitters (Holroyd and Trefry 2011, Klaassen et al. 2014) and documenting sources of mortality would perhaps strengthen our contention that storms are an important source of mortality during migration. Use of satellite transmitters would also help identify the scale at which breeding dispersal typically occurs.

Weather on the Wintering Ground

Our finding that Burrowing Owl apparent survival was affected by factors on the wintering grounds supports the suggestion by Karell et al. (2009) and Salewski et al. (2013) that winter severity could be an overriding factor influencing mortality for many migratory species. For SK, and for all 3 study areas during the period when all were active, there was a 1-yr lag effect on apparent survival of winter precipitation on the wintering grounds. The 1-yr lag effect of winter precipitation could influence mortality probabilities on the wintering grounds or fidelity to the Canadian breeding grounds. The relationship between apparent survival of Burrowing Owls and precipitation on the wintering grounds could have been influenced by the exceptionally wet winter in 1991–1992 (Figure 2). Extreme precipitation could have caused direct mortality of Burrowing Owls and also caused vegetation to reach an unprecedented height and density, thus making prey items less accessible, thereby increasing Burrowing Owl starvation. A recent study by Khalsa (2013) observed that Burrowing Owl abundance on Breeding Bird Survey routes in the Mojave and Sonoran deserts was also weakly, but positively, influenced by a 1-yr lag of winter precipitation. It is possible that when overwintering weather conditions are favorable, Canadian Burrowing Owls may be less likely to

TABLE 4. Models explaining variation in Burrowing Owl apparent survival (Φ) over the period when all 3 study areas in Alberta, Saskatchewan, and Manitoba, Canada, were active, 1989–1993. Model parameters are the same as in Table 1.

	$\Delta QAIC_c$	w_i	K
Φ(sex + study area) p(sex + study area)	0 [a]	0.17438	11
Φ(sex + study area + PrecipWinter1YrLag) p(sex + study area)	0.5474	0.13263	12
Φ(sex + study area + SpringStorms) p(sex + study area)	0.8118	0.1162	12
Φ(sex + study area + FallStorms) p(sex + study area)	1.0341	0.10398	12
Φ(sex + study area + BreedingPrecip) p(sex + study area)	1.1705	0.09712	12

[a] $QAIC_c = 443.5850$.

leave their wintering grounds and more likely to remain after winter to breed in Mexico and the southern United States (Macías-Duarte 2011). Inherent in this explanation is the idea that migration tendency in the Burrowing Owl is relatively plastic (Ogonowski and Conway 2009).

We acknowledge that our estimates of precipitation on the wintering grounds were at a very coarse scale. The observed effects of wintering-ground weather on apparent survival might have been stronger if we could have used information from the precipitation grid cells by overlaying the exact wintering locations of Burrowing Owls from AB, SK, or MB, rather than an average value across the entire potential range of suitable winter habitat areas.

Prey Abundance on the Breeding Ground

Vole and grasshopper irruptions on the breeding grounds did not influence Burrowing Owl apparent survival in Canada. Burrowing Owl nesting success, fledgling production, postfledging survival, and subsequent first-year local recruitment were all positively affected by the 1997 vole outbreak in SK, and we observed a subsequent population increase in 1998 (Poulin et al. 2001, Poulin 2003, Todd et al. 2003, Wellicome 2005). However, it does not appear that adult apparent survival is related to such vole population peaks on the breeding ground. This contrasts with findings by Gervais and Anthony (2003) that adult female Burrowing Owl annual survival, in a non-migratory population, was positively associated with rodent biomass in their diets.

Spatial Variation in Apparent Survival

Differences in the apparent survival of Burrowing Owls among the 3 study areas may be partially attributed to methodological or biological effects of the availability of suitable habitat in each study area. Recapture probability would be biased low if Burrowing Owls were more difficult to relocate in areas with more grassland habitat (e.g., AB), which may interact with the biological reality that individuals in landscapes with a high amount of grassland may disperse farther than individuals in areas with low amounts of grassland (also see Todd et al. 2007). This remains an avenue for future research because, at the time of our mark–recapture studies, information on land use and land cover was not available at the landscape scale. It is also possible that wintering grounds and migration routes differ for Burrowing Owl populations in Alberta, Saskatchewan, and Manitoba. Further research using satellite telemetry would be able to elucidate where individuals from each province migrate and winter.

Although many of the relationships (i.e. directions of effect) between apparent survival and the explanatory variables were consistent across the study areas, a different suite of variables were important. We suspected that these observed differences may have resulted from the duration of the mark–recapture periods, annual sample size in each study area, and the range of values observed within each of the explanatory variables during these periods. This hypothesis was supported by our finding that adult apparent survival was only weakly correlated with the explanatory variables when the mark–recapture study period and sample size were limited (5 yr, 1989–1993). This result highlights the importance of having long-term monitoring data and a large sample size to elucidate potential mechanisms of endangered-species declines. However, it is important to note that the same explanatory variables (PrecipWinter1YrLag, FallStorms, and SpringStorms) and directions of effect were apparent, although weak, in our analysis of the 5-yr dataset.

General Conclusions

Under future climate-change scenarios, storm events (tornados, hail, and thunderstorm winds) are predicted to increase along the Burrowing Owl migration route between prairie Canada and central Mexico (Diffenbaugh et al. 2013), whereas annual rainfall is predicted to decrease on wintering grounds in northern and central Mexico (Peterson et al. 2002). Our study suggests that such changes will have negative and positive influences, respectively, on Burrowing Owl apparent survival measured in prairie Canada, and quite possibly for many other migratory Burrowing Owl populations in the northern portion of their continental range. However, the ultimate influence of such changes in apparent survival on the overall population decline of Burrowing Owls in Canada have yet to be quantified. Nonetheless, given that the number of Burrowing Owl pairs remaining in Canada is already quite low, any severe stochastic events that have negative effects on apparent survival, even during only 1 yr, present a serious risk to the Canadian population. For example, extreme rain events occurred in much of the northern Great Plains during the spring of 2011 (NOAA, http://www.ncdc.noaa.gov/temp-and-precip/maps.php). That year, we found that only 9 nesting pairs returned to the SK study area—a population decrease of 92% from the previous year. Future research may be able to elucidate the contribution of variables that affect adult apparent survival in relation to factors (e.g., weather or habitat change) that influence the number of Burrowing Owls that immigrate each year into Canada, as well as the contributions of reproduction and local recruitment to population change of Burrowing Owls in Canada. When the relative contributions of each of these demographic parameters to Burrowing Owl population growth are understood, they can then be used to understand the effects of a changing climate, outside of the breeding grounds, on Burrowing Owls in Canada.

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