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# Migration routes and timing of Mountain Plovers revealed by geolocators

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ABSTRACT. Understanding the migratory movements and habitats used during the annual cycle of migrants is essential to developing comprehensive conservation strategies. Mountain Plovers (*Charadrius montanus*) are short-distance migrants listed as a species of conservation concern in many states across their range, however, little is known about their migratory ecology. We used data from geolocators to describe the first direct estimates of migratory routes and migration schedules for Mountain Plovers breeding in Phillips County, Montana. We attached geolocators to 36 Mountain Plovers in 2010–2012 and recovered five (13.9%; three males and two females). Four of five Mountain Plovers in our study overwintered in Texas, and one overwintered in Arizona. Migration routes were relatively linear, with the exception of one plover that moved south and then west to reach its winter range in Arizona. Two plovers left breeding areas in mid-July and the other three left in late September. All plovers used stopover sites near either eastern Colorado or southwest Kansas. Plovers that departed earlier used stopover sites for ~100 d, whereas those that left later used them for ~35 d. All plovers in our study arrived in wintering areas by early November and departed by late March. Our results suggest that eastern Colorado and southwest Kansas are important stopover areas during migration, and highlight the need to better understand how these locations support non-breeding plovers.

RESUMEN. **Las rutas migratorias y el calendario de migración del Chorlito llanero revelados por geolocalizadores**

La comprensión de los movimientos migratorios y los hábitats utilizados durante el ciclo anual de los migrantes es esencial para el desarrollo de estrategias de conservación integrales. Los chorlitos llaneros (*Charadrius montanus*) son migrantes de corta distancia que son especies de interés para la conservación en muchos estados en su área de distribución, sin embargo, sabemos poco de su ecología migratoria. Usamos los datos de geolocalizadores para describir las primeras estimaciones directas de las rutas migratorias y del calendario de migración para los chorlitos que se reproduce en el condado de Phillips, Montana, EEUU. Colocamos geolocalizadores en 36 chorlitos en 2010–2012 y recuperamos cinco (13.9%; 3 machos y dos hembras). Cuatro de los cinco chorlitos invernaron en Tejas, y otro chorlito paso el invierno en Arizona. Las rutas migratorias fueron relativamente lineal, con excepción de un chorlito que mudó al sur y después al oeste para llegar a su zona invernal. Dos chorlitos salieron de sus zonas de reproducción a mediados de julio y los otros tres salieron a finales de septiembre. Todos los chorlitos usaron áreas de descanso cerca del este de Colorado o del suroeste de Kansas. Los chorlitos que empezaron la migración más antes usaron áreas de descanso por ~100 días, en cambio los chorlitos que salieron mas tardes usaron las áreas por ~35 días. Todos los chorlitos en nuestro investigación llegaron a las áreas invernales a principios de noviembre y salieron a los finales de marzo. Nuestros resultados indican que el este de Colorado y el suroeste de Kansas son áreas de descanso importantes durante la migración, y señala la necesidad de para comprender mejor como estas áreas soportan a los chorlitos que no son reproductivas.

*Key words: Charadrius montanus*, geolocator, light-level archival tag, migration phenology, migration routes, stopover

Mountain Plovers (*Charadrius montanus*) are short-distance migrants listed as a species of conservation concern in many states across their range due in part to apparent declining populations (Colorado Division of Wildlife 2003, Andres and Stone 2009). Conservation efforts have largely focused on management of breeding habitats, but population dynamics are also influenced by adult survival, particularly during migratory periods, a period about which little is known (Dinsmore et al. 2010).

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The breeding range of Mountain Plovers extends along the western edge of the Great Plains, concentrated mainly in Colorado, Wyoming, and Montana (Andres and Stone 2009). Known overwintering locations include desert and agricultural settings in the Central and Imperial valleys of California and along the border of the United States and Mexico (Knopf and Rupert 1996, Wunder and Knopf 2003; Fig. 1). The largest aggregations of wintering plovers are thought to occur in California, with smaller concentrations in Arizona, Texas, and northern Mexico (Knopf and Rupert 1995, Knopf and Wunder 2006).

Previous studies involving the use of color banding and stable isotopes (Knopf and Rupert 1995, Wunder 2007) have elucidated some aspects of Mountain Plover migration. Individuals return annually to the same breeding areas, suggesting high breeding-site fidelity, but plovers from populations across their breeding range intermix at overwintering sites in loosely structured flocks. Mountain Plovers overwintering in California begin migrating in early March (Knopf and Rupert 1995) and start arriving at breeding areas from mid-March through mid-April, with earlier arrivals on the plains of eastern Colorado and later in central Colorado mountain parklands and more northern sites such as Montana (Knopf and Wunder 2006). Spring migration appears to be relatively rapid, whereas fall migration appears to be more prolonged. Most plovers leave breeding areas by August, with some post-breeding flocks persisting in central and eastern Colorado until mid-September. Plovers arrive in California and Texas starting in mid-October, with sightings in Mexico by November (Knopf and Wunder 2006). Migration routes and potential stopover areas are largely unknown. The lack of information about Mountain Plover migration limits development of comprehensive conservation strategies and our understanding of their full annual cycle life history.

Recent miniaturization of bird-borne tracking technologies, particularly small light-level archival tags (geolocators), are providing new insight about migratory phenology and routes

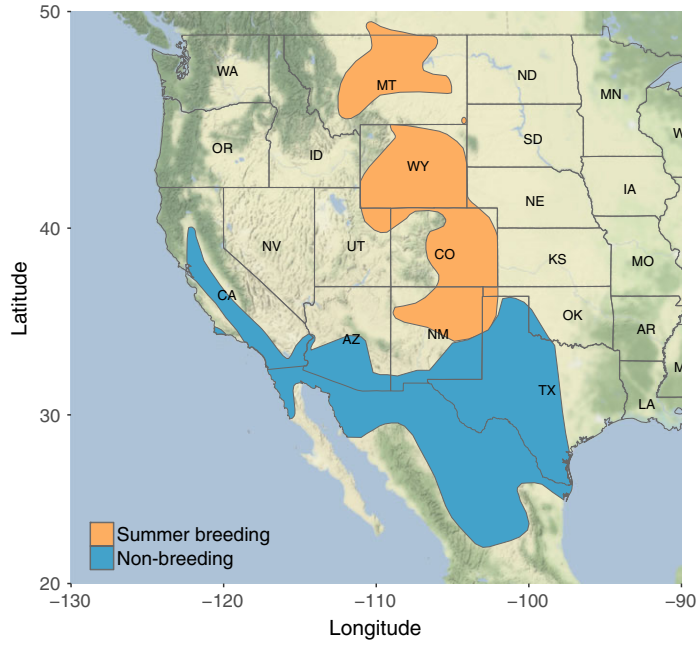


Fig. 1. Mountain Plover breeding (lighter shading; orange) and non-breeding (darker shading; blue) ranges. The non-breeding range includes areas where plovers have been observed during migration. Ranges adapted from NatureServe (Ridgely et al. 2003) and Andres and Stone (2009). [Color figure can be viewed at wileyonlinelibrary.com]

as well as behavior and landscape use during migration (e.g., Stutchbury et al. 2009, Bächler et al. 2010, Ryder et al. 2011, Johnson et al. 2012, Stanley et al. 2012, Hallworth et al. 2015). Although light-level geolocation data are less precise than GPS data (Phillips et al. 2004, Rakhimberdiev et al. 2016), the devices are light-weight and provide more information about migration timing and routes than mark-recapture techniques for species too small for GPS tags. Using geolocators, our objectives were to describe and characterize the migration routes and migration phenology of Mountain Plovers breeding in Phillips County, Montana.

## METHODS

We studied Mountain Plovers at black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Phillips County, Montana, from 2010 to 2015 (see Dinsmore et al. 2002 for description of the study area). From mid-May through early August, we searched prairie dog colonies for plover nests and captured nest-tending adults with walk-in traps placed over nests. After the breeding season, we searched for plovers at night using a spotlight and captured them with a large dip-net. Plovers were marked with a unique combination of colored leg bands and a numbered aluminum U.S. Geological Survey band affixed to the tibiotarsus. We also measured body mass with a Pesola spring scale ($\pm$ 1 g), and collected either a blood or feather sample from each captured plover to determine sex (AvianBiotech International, Tallahassee, FL).

We fitted each captured bird with a 3-g light-level geolocator (~3% of average plover body mass; LightBug, Lotek, Inc., Newmarket, ON, Canada). Geolocators were attached with a leg-loop harness made of Teflon ribbon and rested on the birds' backs. We attached geolocators to 36 Mountain Plovers, including 15 in 2010 (2 June to 2 August), nine in 2011 (4 July to 3 August), and 12 in 2012 (1 June to 12 July). Ten geolocators deployed in 2010 also had small radio-transmitters to facilitate relocation efforts.

We determined sunrise and sunset times from the raw light-level data using the website tool TAGS (Totally Awesome Geolocator Service; http://tags.animalmigration.org) with a light intensity threshold set at 280 (range = 1–3000 on an arbitrary scale). Light data were plotted and visually inspected for misidentified sunrise and sunset times; all corrections were logged by TAGS. Data were exported for further analysis in R (R Core Team 2014) using the R-package "GeoLight" (Lisovski and Hahn 2012) to determine stationary periods and migratory routes.

Using "GeoLight", we estimated longitude and latitude positions twice for each 24-h period from day/night length and local solar noon/midnight using a sun elevation angle individually calibrated from the first 2 weeks of sunrise and sunset data when we assumed plovers were close to the deployment site. Near equinox events, as the solar declination angle approaches zero, latitude estimates are heavily biased north or south so we censored position estimates under 0.15 of the sine of solar declination angle. We approximated migratory routes by applying a loess smoother function (smoothing span = 0.3) to estimated longitude and latitude positions to reduce noise in position data and simplify data visualization. We assigned stationary sites by identifying change-points in sunrise and sunset data for each tag using a probability of change threshold of 0.95 and sites that were overlapping or within 250 km of each other were merged.

We created a map for each individual by combining the estimated path with 50% kernel density estimates (KDE) of positions from extended stationary periods. Kernel densities were calculated using the "adehabitatHR" package in R (Calenge 2006). Segments of migratory routes that could not be calculated due to equinox events were approximated based on calculated positions prior to and following the event. We calculated migration distance as the orthodromic (great circle) distance between centroids of the KDE polygons and derived migration speed by dividing this distance by the number of days between migration departure and arrival, including days spent at stopover sites. Days spent at stopover sites were included so that migration speed was reflective of the overall migration process.

## RESULTS

Of 36 geolocators deployed, we recovered five (13.9%; three males and two females) during the subsequent breeding season

(Table 1); eight additional tagged plovers were resighted, but not recaptured, so the overall return rate was 36.1%. Fall migration routes and KDEs of extended stationary sites for each bird are shown in Fig. 2. We were unable to estimate complete spring migration routes for three individuals (C, D, and E) because migration occurred close to the vernal equinox when latitude estimates are biased south and the geolocators stopped recording data shortly after they initiated migration. We recovered enough data to estimate a partial route for Plover B and report an approximate route based on the last estimated location and where the tag was recovered on the breeding site.

In 2010, plovers A and B left the breeding grounds in mid-July and stopped in eastern Colorado (Fig. 2; Table 1). Plover A remained in Colorado for ~100 d before arriving in east-central Texas for the winter. Plover B remained in Colorado for ~10 d, then moved to a second stopover site in the panhandle region of Oklahoma and Texas where it remained for ~92 d before moving to east-central Texas for the winter. These plovers arrived in the same general wintering range in Texas on 24 (bird A) and 26 (bird B) October, respectively, and both remained there for ~100 d. Birds A and B initiated spring migration on 21 and 20 March, respectively. Plover A returned to the breeding site on 24 April 2011. There was insufficient data to estimate spring arrival dates for the other four plovers.

The other three plovers (C, D, and E) initiated fall migration much later in 2011 and 2012, staying in Montana until late September. These three birds also used stopover sites, but for shorter periods (34 to 40 d). The timing of winter arrival dates was within a week of those for early migrants A and B (Table 1). The timing of departure relative to the fall equinox limited our ability to precisely estimate the geographic coordinates of stopover areas because of the error associated with estimating latitude when there is minimal or no change in day length. This effect is clearly demonstrated by the large KDE areas in Fig. 2. Plover D was the only bird that did not overwinter in central Texas, instead moving southwest across northern New Mexico into Arizona for the winter. Plovers C, D, and E departed for breeding areas in late March, near the vernal equinox.

The average fall orthodromic migration distance for all five plovers was 2000 ± 215 (SD) km and the average migration speed was 38 ± 15 km $d^{-1}$. The bird with the shortest migration distance (1668 km) had the shortest stopover period (34 d), and the bird with the longest distance (2165 km) had the longest stopover (100 d; Table 1). Spring migration distance for Plover A was 1222 km, with a migration speed of 37 km $d^{-1}$ (Table 1). We had insufficient data for

Table 1. Fall migration phenologies for Mountain Plovers that bred in Phillips County, Montana, based on geolocator data collected from returning birds. Fall migration speeds include time spent at stopovers.

| Fall migration | A (male) | B (male) | C (female) | D (female) | E (male) | Mean |
|---|---|---|---|---|---|---|
| Breeding departure | 14 Jul 2010 | 13 Jul 2010 | 22 Sep 2011 | 28 Sep 2012 | 22 Sep 2012 | 26 Aug |
| Winter arrival | 24 Oct 2010 | 26 Oct 2010 | 3 Nov 2011 | 3 Nov 2012 | 30 Oct 2012 | 20 Oct |
| Stopover (d) | 100 | 92 | 40 | 35 | 34 | 60 |
| Overwinter (d) | 148 | 145 | 133 | 136 | 141 | 140 |
| Fall migration distance (km) | 2165 | 2158 | 1898 | 2111 | 1668 | 2000 |
| Fall migration speed (km $d^{-1}$) | 21 | 21 | 45 | 59 | 44 | 38 |
| Spring migration distance (km) | 1222 | – | – | – | – | 1222 |
| Spring migration speed (km $d^{-1}$) | 37 | – | – | – | – | 37 |

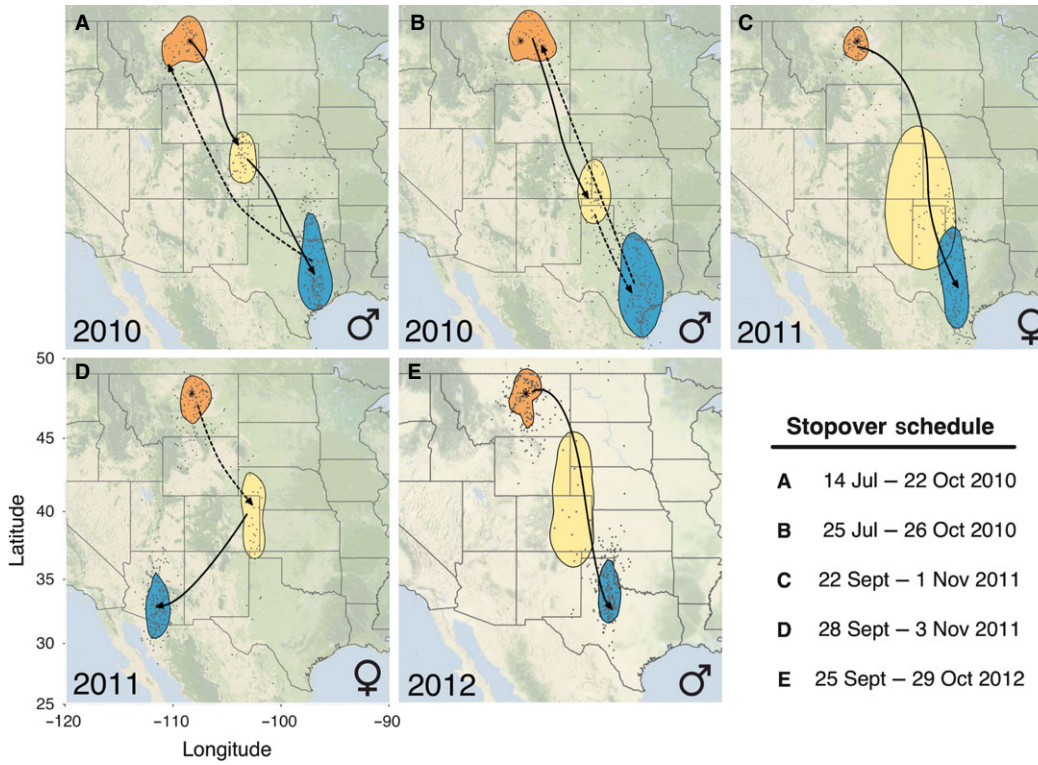


Fig. 2. Geolocator-based migration routes and overwintering ranges for five Mountain Plovers (A–E) that bred in Phillips County, Montana. Each figure depicts post-breeding (mid-tone shading; orange), stopover (lightest shading; yellow), and overwintering (darkest shading; blue) regions. Deployment locations are indicated by an asterisk. Loess smoothed migration routes are represented by arrows, dashed routes are approximated from positions proceeding and following the equinox. Stopover arrival and departure dates are provided in the lower right corner; see Table 1 for breeding and overwinter schedule.

tags B-E to calculate spring migration distance and speed.

## DISCUSSION

Four of five Mountain Plovers in our study overwintered in Texas, and one overwintered in Arizona. Migration routes were relatively linear, with the exception of the plover that moved south and then west to reach its winter range in Arizona. Departure times from breeding areas varied among plovers, as did use of stopover sites en route to winter destinations. Average fall migration speed for Mountain Plovers in our study was similar to that for spring migration (Table 1). However, the average distance and duration of migration were longer in the fall than in the spring, suggesting that plovers likely made many short flights during both migration periods, but did not spend extended periods in areas between flights in the spring. A study of Little Ringed Plovers (*Charadrius dubius*) revealed similar patterns (Hedenström 2013), however, Little Ringed Plovers are long-distance migrants and thus travel greater mean fall migration distances (6252 km) at a faster mean fall migration speed (133 km $d^{-1}$). Mean fall migration speeds and distances of Mountain Plovers were comparable to those reported for Eurasian Golden Plovers (*Pluvialis apricaria*), short-distance migrants (1870 km and 18 km $d^{-1}$, respectively; Machín et al. 2015).

No plovers in our study overwintered in California despite previous reports that the Central and Imperial valleys in California support > 50% of the overwintering

population of Mountain Plovers (Knopf and Rupert 1996, Andres and Stone 2009). Moreover, Christmas Bird Count (CBC) data from corresponding years reveal that more plovers were recorded in Texas than in California during the 2011 and 2012 winters (Fig. 3), and plovers were not reported on counts in any other states during those years. Plovers overwintering in Texas use coastal prairies, agricultural fields, and alkaline flats, habitats similar to those used in the California valleys, and Andres and Stone (2009) suggested that the proportion of the population wintering in Texas was underreported. Although based on a small sample size, our results support this suggestion.

Differences among Mountain Plovers in overwintering locations have been reported previously using individual color marking and stable isotope analysis (Knopf and Rupert 1995, Wunder 2007). These authors also documented mixing of individuals from different breeding populations in wintering areas, but provided no information concerning possible variation in migratory timing or routes. We observed variation in departure dates from the breeding grounds, with two plovers leaving Montana in mid-July (2010) and three others leaving in late September

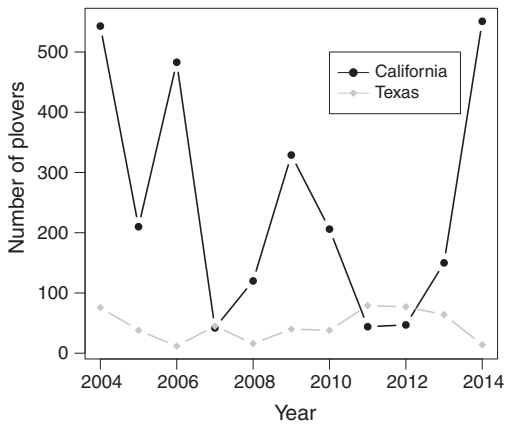


Fig. 3. Count data for Mountain Plovers recorded from Christmas Bird Count (CBC) circles for California and Texas. CBC data are provided by the National Audubon Society and through the generous efforts of Bird Studies Canada and countless volunteers across the western hemisphere (See www.audubon.org and www.christmasbirdcount.org for more information).

(2011 and 2012). Knopf and Wunder (2006) suggested that Mountain Plovers may leave breeding areas after breeding attempts fail or young fledge. However, none of the five plovers in our study fledged young, so differences in departure dates were not due to differences in nest fate.

More likely, differences among years in environmental conditions explain the observed differences in departure times among years. The Great Plains of North America experience sudden and severe weather fluctuations. Such perturbations can affect strategies of migratory birds, particularly short-distance migrants that may respond facultatively to changing migratory cues (Forchhammer et al. 2002). For example, winter cold spells can induce migratory movements in Eurasian Golden Plovers, a short-distance migratory shorebird (Machín et al. 2015). To examine potential weather effects, we obtained daily weather data from the National Oceanic and Atmospheric Administration's Global Historical Climatology Network-Daily dataset (Menne et al. 2012). Three National Weather Service stations included in this dataset are approximately equidistant from our study area (mean distance = ~33 km), so we averaged daily measures across the three stations (located at 47°55′3.72″N, 108°31′37.56″W; 47°50′30.48″N, 107°57′20.16″W; and 47°34′39″N; 108°43′41.88″W). There were no apparent trends in daily temperature preceding or following departure dates, however, average July maximum and minimum temperatures were lower in 2010 than in 2011 and 2012, and average maxima remained lower in August and September (Fig. 4A and B). Although July maxima and minima were lower in 2010, they were still higher than maxima and minima in September 2011 and 2012 when plovers C, D, and E departed the breeding area. Together, daily and monthly trends suggest temperature is not the sole environmental cue prompting departure, but it may be correlated with other processes related to resource availability that affect migration phenology. Average July precipitation in 2010 did not differ from that in 2012, but was higher in 2011 (Fig. 4C), suggesting that intense rainstorm activity likely did not account for the early departure of Plovers A and B in 2010.

An alternative explanation for early departure from breeding areas and variation in stopover duration could be related to energetic needs associated with prebasic molting schedules. For example, other shorebirds undertake a molt migration, including Long-billed Dowitchers (*Limnodromus scolopaceus*; Barbaree et al. 2015), Curlew Sandpipers (*Calidris ferruginea*; Barshep et al. 2013), Purple Sandpipers (*Calidris maritima*; Summers et al. 2004), and Grey Plovers (*Pluvialis squatarola*; Branson and Minton 1976). Mountain Plovers molt remiges and coverts during prebasic molt after the breeding season, starting in mid-June and completing by mid- to late August (Knopf and Wunder 2006). Plovers may leave breeding areas earlier and either delay or suspend molt until arrival at a stopover location that provides higher-quality habitat, greater food availability, or reduced competition. Annual variation in climate can affect arthropod abundance and density as well as the timing of peak availability. Fluctuation in the abundance of grasshoppers, one of the main prey of Mountain Plovers, can be influenced by temperature and precipitation; favorable conditions are generally characterized by warmer and dryer conditions (Belovsky and Slade 1995, Branson 2008, Jonas et al. 2015). The relatively cooler summer temperatures in 2010 may have had some effect on food availability, potentially prompting Plovers A and B to depart earlier in search of stopover areas with more prey to initiate or complete their basic molt. However, the accuracy of light-level geolocation precludes identification of specific habitats used by plovers during stopovers in our study and we have no direct evidence of delayed molt; in Colorado and Montana, we regularly observe flight feather molt during late incubation. Nevertheless, our results identify eastern Colorado and southwest Kansas as important stopover areas used for extended periods and unknown reasons.

Variation in habitat quality and food resources in wintering areas can contribute to individual variation in spring departure schedules (Studds and Marra 2011). The few birds tracked in our study, however, exhibited little variation in spring departure dates and departed close to the vernal equinox, suggesting that photoperiod cues may be stronger

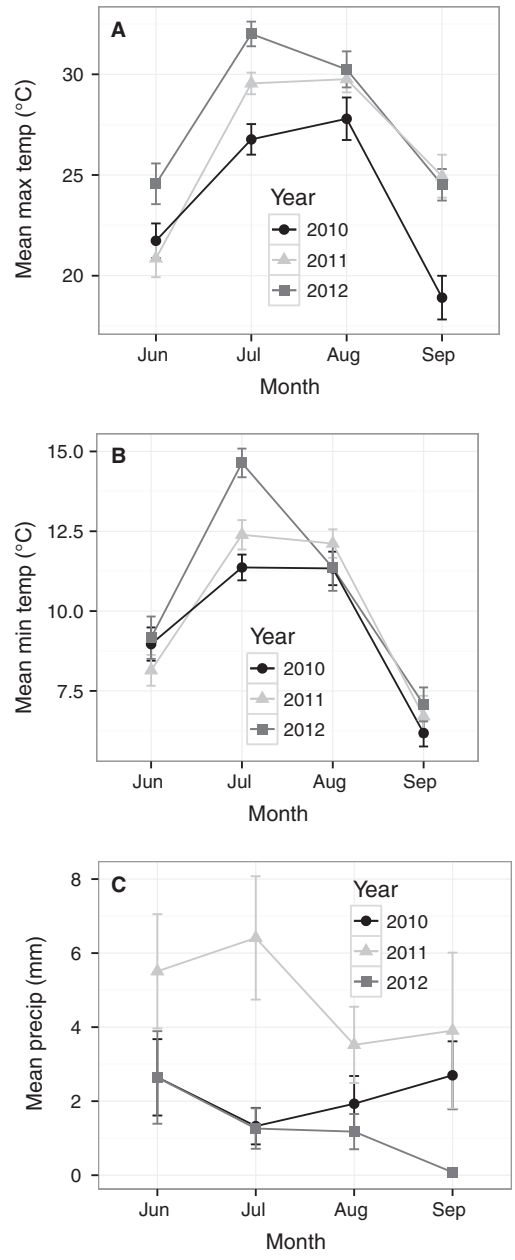


Fig 4. Monthly mean (± SE) maximum temperature (A), minimum temperature (B), and precipitation (C) at the breeding site of Mountain Plovers in Phillips County, Montana, during the summer months (June–September) from 2010 to 2012. Monthly means were derived from daily measurements averaged across three National Weather Service weather stations closest to the study area (mean distance = ~33 km).

predictors of spring migratory timing for plovers that breed in Montana.

Although our results improve our understanding of Mountain Plover migration, questions remain concerning factors that influence the timing of fall migration, variation in stopover duration, and where plovers choose to overwinter. Continued advancements and miniaturization in tracking technologies will provide expanded opportunities to track individuals, explore the drivers of variation in plover migration, and provide continued insight for development of conservation strategies. If recent population models are correct (Dinsmore et al. 2010), and Mountain Plover populations are in part limited by adult survival during migration, identification of important stopover habitats that support plovers during fall migration will help in the development of more comprehensive conservation strategies.

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