Incubation patterns of a shorebird with rapid multiple clutches, the Mountain Plover (*Charadrius montanus*)

P.D.B. Skrade and S.J. Dinsmore

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Abstract: The rapid multiclutch parental care system of the Mountain Plover (*Charadrius montanus* J.K. Townsend, 1837) presents a rare opportunity to examine sex-specific differences in avian uniparental care. We monitored incubation activity for this species using a combination of video (857 h at 25 nests during 2007) and temperature data-recording (>10 000 h at 124 nests during 2006–2008) at breeding areas in Montana. We modeled possible differences in nocturnal activity using the duration of off-bouts of incubating adults and included the effects of nest age, day of season, ambient temperature, precipitation, and time of departure. Males, on average, made 1.48 departures·h^{-1} over a 24 h period (SE = 0.35 departures·h^{-1}, n = 6 days) and females made 1.41 departures·h^{-1} (SE = 0.11 departures·h^{-1}, n = 26 days). The mean duration of nocturnal off-bouts for males was 0.38 h (SE = 0.01 h, n = 1925), while the mean duration of female off-bouts was 0.36 h (SE = 0.01 h, n = 2716). Plovers had longer off-bouts from their nests in the middle of the night and early in the breeding season. This study furthers an understanding of incubation patterns in an uncommon avian parental care system and provides important behavioral information about a species of conservation concern.

Résumé : Le système de soins parentaux à couvées multiples rapprochées du pluvier montagnard (*Charadrius montanus* J.K. Townsend, 1837) représente une occasion rare d'examiner les différences liées au sexe dans les soins uniparentaux chez les oiseaux. Nous avons suivi l'activité d'incubation chez cette espèce avec une combinaison d'enregistrements vidéo (857 h à 25 nids durant 2007) et d'enregistrements de mesures de température (>10 000 h à 124 nids durant 2006–2008) dans des aires de reproduction au Montana. Nous avons modélisé les différences possibles d'activité nocturne à partir des durées des interruptions d'incubation par les adultes; nous avons inclus les effets de l'âge du nid, du jour de la saison, de la température ambiante, des précipitations et du moment du départ du nid. Les mâles quittent le nid en moyenne 1,48 fois·h^{-1} sur une période de 24 h (ET = 0,35 fois·h^{-1}, n = 6 jours) et les femelles 1,41 fois·h^{-1} (ET = 0,11 fois·h^{-1}, n = 26 jours). La durée moyenne des interruptions nocturnes chez les mâles est de 0,38 h (ET = 0,01 h, n = 1925), alors que la durée moyenne des interruptions chez les femelles est de 0,36 h (ET = 0,01 h, n = 2716). Les pluviers ont des périodes d'interruption plus longues au milieu de la nuit et tôt dans la saison de reproduction. Notre étude améliore notre compréhension des patrons d'incubation dans un système de soins parentaux peu commun et fournit d'importantes observations sur le comportement d'une espèce dont la conservation est préoccupante.

[Traduit par la Rédaction]

Introduction

While caring for their young, individuals must constantly weigh the costs and benefits of their current reproductive effort relative to those of future efforts (Clutton-Brock 1991). One decision an incubating bird must make is at what time and for how long it can leave its nest, balancing inhibition of embryonic development and survival of the nest with tending to its own needs. Periodic cooling of an egg during off-bouts (end of an incubation period) from the nest can severely hinder development and impact embryonic metabolic processes (Olson et al. 2006). Additionally, increased activity at the nest can increase the risk of predation (Martin et al. 2000; Muchai and du Plessis 2005). Thus, the incubating adult must not make too many departures from the nest or allow the eggs to cool. However, if the nest is left exposed in a hot environment, the eggs can become overheated and inviable (Bennett and Dawson 1979; Grant 1982). In particularly hot areas, incubating ground-nesting birds will shade their eggs and cool themselves by gular fluttering (Amat and Masero 2004), which prevents the eggs from overheating but confines the bird to the nest, often for extended periods. If an incubating bird is unable to leave its nest during the day because of the threats of exposure or predation of its eggs, then as a result they will forage during the night (McNeil et al. 1992).

Among shorebirds (Charadriiformes) there is a variety of parental care systems ranging from biparental, where both parents share in the tasks of incubation and brood-rearing, to uniparental care by either males or females (Oring 1986; Reynolds and Székely 1997). In a few species, such as Tem-

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minck's Stint (*Calidris temminckii* (Leisler, 1812)) and the Mountain Plover (*Charadrius montanus* J.K. Townsend, 1837), the female lays her first clutch of eggs in a shallow scrape on exposed ground and it is tended entirely by the male (Graul 1975; Hildén 1975). She then lays a second 3-egg clutch at a different location that she tends alone. This method of parental care is known as a rapid multiclutch system and it provides an interesting opportunity to examine sex-specific differences in nest attendance. In this situation, the other member of a pair is unable to relieve the incubating parent through mate-feeding (Martin and Ghalambor 1999) or by sharing incubation responsibilities (Ketterson and Nolan 1994), and so the incubating adult must constantly consider its parental investment (Clutton-Brock 1991).

We examined uniparental nocturnal incubation behavior in relation to the sex of the incubating adult, the stage of incubation, the day of the nesting season, and the effect of the previous day's weather using nesting Mountain Plovers. This is a species of conservation concern that nests in open, flat, disturbed areas of the Great Plains and Great Basin (Knopf and Wunder 2006). There is evidence that incubating Mountain Plovers are active during the night, but this has not been quantified. Similar to other shorebirds (Wallander 2003), nesting Mountain Plovers have been observed away from their nests throughout the night (Graul 1975; S.J. Dinsmore and P.D.B. Skrade, personal observation), although these observational data are insufficient to firmly establish nocturnal activity patterns.

We first wished to test the hypothesis that the sexes will exhibit differing incubation patterns. Both parents have similar incubation responsibilities; however, previous studies found that nests attended by male Mountain Plovers have greater nest survival than females (0.49 for males, 0.33 for females; Dinsmore et al. 2002). Predation is the main cause of nest failure for this species (Knopf and Wunder 2006) and this difference in nest survival could be attributed to the slightly earlier initiation dates of male-tended nests, with predators cueing in to the possible food source later in the season. It could instead be a result of differing incubation behaviors such as males taking longer recesses or females making more frequent departures. Skutch (1949) hypothesized that increased activity at the nest owing to the feeding of altricial young during brood-rearing attracted attention to the nest, leading to a higher depredation rate than in the incubation stage. Although this hypothesis can potentially be explained by the begging calls of the nestlings (Haskell 1994), other studies suggest that this is a result of differential activity (Muchai and du Plessis 2005). Body condition has been shown to influence incubation activity in uniparental systems (Wiebe and Martin 2000). If female Mountain Plovers have higher energy expenditure during the laying stage than males, as in the closely related Killdeer (*Charadrius vociferus* L., 1758) (Brunton 1988), then perhaps they will require more departures from the nest to forage than males.

We next tested the hypothesis that the previous day's weather conditions would influence the duration of nocturnal off-bouts from the nest. Mountain Plover eggshells are darkly colored and exceptionally thick for the subfamily Charadriinae (Graul 1975), and are cold tolerant but also susceptible to overheating (Knopf and Wunder 2006). During periods of high ambient temperature and solar radiation, the tending adult is often found exhibiting cooling behaviors (S.J. Dinsmore and P.D.B. Skrade, personal observation) and is constrained to the nest much the same as when it rains (S.J. Dinsmore and P.D.B. Skrade, personal observation). We hypothesized that incubating birds would make longer off-bouts during nights following such conditions (high ambient temperatures and precipitation).

Finally, we tested the hypothesis that incubation behavior differed through time, not only in a 24 h period but across days, during incubation and throughout the breeding season. A previous study of the breeding biology of the Mountain Plover showed a tendency for daily nest survival to increase as a function of nest age (Dinsmore et al. 2002). The improved survival might be a result of a change in the incubation pattern, because during the day incubating adults spent more time at the nest as the eggs near hatching (Graul 1975). We expected that birds would spend less time away from their nests as nest age increased. We monitored nocturnal nest attentiveness of Mountain Plovers, but we sought to minimize disturbance to this species of conservation concern. Recent studies validated the use of temperature data loggers to measure survival of songbird nests (Weidinger 2006) and to indicate the onset of incubation and timing of nest failure in shorebirds (Hartman and Oring 2006). However, few studies have used this method to examine incubation activity of ground-nesting shorebirds (Tulp and Schekkerman 2006; Schneider and McWilliams 2007) and so we used a combination of video monitoring and temperature data loggers to quantify nocturnal incubation patterns of this species.

Materials and methods

Study area

We studied incubation activity of Mountain Plovers using remote data loggers during three consecutive breeding seasons (2006–2008) and continuously video-monitored a small sample of nests during the 2007 breeding season. All observations were made in an approximately 3000 km^2 area located in southern Phillips County in north-central Montana (47°40′N–47°55′N, 107°35′W–108°30′W). This area experiences high ambient temperature fluctuations in the summer months, often ranging from below 10 °C to above 40 °C (NOAA 2006, 2007, 2008). In our study area, Mountain Plovers nest almost exclusively on colonies of black-tailed prairie dog (*Cynomys ludovicianus* (Ord, 1815)) (Knowles et al. 1982; Knowles and Knowles 1984; Dinsmore and Knopf 2005).

Nest searching and monitoring

Fieldwork each year began in mid-May and continued until the end of the birds' nesting season, usually late July or early August. Nest searching techniques were similar across years and followed those described by Dinsmore et al. (2002). Once found, we checked nests every 3–7 days until they had hatched or failed, and estimated all egg ages by examining their specific gravity in a column of water (Westerskov 1950).

Capture and marking of Mountain Plovers generally followed the procedures described in Dinsmore et al. (2002). We captured nest-tending adult plovers using a walk-in trap constructed of chicken wire and placed over the nest. When

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birds were in hand, we took feather and blood samples for future analysis and genetic sexing and each plover was leg-banded with an aluminum USGS size 3A band and a unique combination of four colored bands. Because these plovers are sexually monomorphic and cannot be reliably sexed at a distance or in hand, sex was determined from feather or blood samples by Avian Biotech International (Tallahassee, Florida, USA) using molecular techniques outlined in Dinsmore et al. (2002). This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol No. 5-06-6129-Q.

Video camera deployment and monitoring

We recorded incubation behavior at 25 nests of 24 incubating Mountain Plovers during the 2007 field season. We used a high resolution closed circuit video camera (Fieldcam type DHD4PTLV160/MIDICAM field television system assembled by Fuhrman Diversified Inc., Seabrook, Texas, USA) with a side-mounted 36 LED array infrared lamp to record 24 h activity at the nest. We mounted the camera on a 1.2 m piece of rebar that was partially buried so that the lens of the camera housing was 0.7 m above ground and 1.9 m to the south of the nest. Placing it to the south of the nest ensured consistent light exposure and allowed us to note the direction the incubating adult traveled when leaving and returning to the nest.

We recorded video imaging at 15 frames·s^{-1} and at 704 pixels × 480 pixels onto an IDE hard drive in a digital video recorder. The recorder was housed in a weatherproof case (0.45 m × 0.35 m × 0.15 m) connected to the camera by a 50 m cable, although the case and the two 12 V, 100 Ah deep-cycle batteries used to power the system were placed in the nearest depression or behind an inactive prairie dog mound. We sprayed the cable once a week and after heavy rain events with Ropel® liquid animal repellent to prevent it from being damaged by prairie dogs. We camouflaged the digital video recorder case and batteries with burlap.

To minimize the possibility of nest abandonment and avoid possible behavioral changes owing to recent handling, we only used the camera at nests of previously color-banded individuals and were able to deploy the system in less than 20 min. We removed the video monitoring system after 24 h unless we were unable to reach the nest because of inclement weather. We selected nests for video monitoring at random, but sometimes deviated from this approach because of logistical constraints or a desire to better balance the sample with respect to sex of the nest-tending adult or nest age.

Data logger deployment and recording

We used 11 HOBO H8 external temperature data loggers (model H08-002-02; Onset Computer Corporation, Bourne, Massachusetts, USA) to monitor 124 Mountain Plover nests from 117 individuals over the 3 years of the study (2006: $n = 31$; 2007: $n = 64$; 2008: $n = 29$). Three loggers were used in 2006 and eight more were purchased prior to the 2007 field season. Each logger consisted of an internal sensor housed in a 6.1 cm × 4.8 cm × 2.03 cm case with an additional 30.5 cm external sensor cable. We coated each data logger case in paraffin wax and placed them in small resealable plastic bags along with a small amount of Drierite® (anhydrous calcium sulfate, $CaSO_4$) desiccant to prevent the loggers from becoming wet.

We carefully placed the logger at each nest site while the eggs were removed from the nest to determine nest age. Starting in the nest contents, we dug a shallow trench (approximately 5 cm × 35 cm) away from the nest and arranged the data logger so that the tip of the external probe was in the center of the nest. We then buried the logger and the cable from the probe, covering the portion of the probe in the nest with a thin layer of nesting material before replacing the eggs. This entire process took 3–5 min depending upon soil compaction.

In 2006, we recorded nest temperature every 30 s, continually recording and overwriting the oldest data from deployment until collection, and yielding 1 day and 9 h of data with at least one full night of observations. The loggers were set to continuously overwrite so that any effects of human disturbance from capture and marking, data logger deployment, or visits to check nest status would not be included in the observation. However, because of the continuous overwriting, occasionally all incubation behavior was lost if eggs hatched or a nest was depredated >33 h before logger retrieval. After reviewing video recordings of behavior during the first week of 2007, we decided that a time delay of 2 h for the temperature data loggers would allow the bird sufficient recovery time from human disturbance. We also increased the recording time to once every minute because departures could easily be determined from a small number of in-field examinations of concurrent temperature and video recordings of this duration. This also increased the sampling time for each nest to 2 days and 18 h before the memory was exhausted.

We attempted to select nests for data logger monitoring at random, but this was difficult because of logistical constraints and because we often did not know the sex of the tending adult until after nesting was completed. Thus, we opportunistically monitored some nests and attempted to maintain a balanced sample of known-sex and known-age nests throughout each nesting season. This approach also resulted in multiple samples of the same bird within a nesting season, although never on consecutive days.

Data preparation

We used a two-step process to validate the temperature logger data and incorporate the information into our analyses. We began by carefully reviewing the video data and noting times when the bird first appeared in or left the camera view. We considered a bird to be "on the nest" when the adult walked over the nest and then settled with its legs apart.

We used two computer programs, both obtained from the Cornell Lab of Ornithology (Ithaca, New York, USA), to define nest departures and their duration for incubating Mountain Plovers from the data loggers. Program RHYTHM (Cooper and Mills 2005) was used to convert temperature data files from data loggers into bioacoustic files, which are usually used to examine bird songs and calls. This program generates departure and arrival times by using different criteria determined by the observer. It detects these using the minimum length of off-bouts, the minimum temperature decrease to be considered an off-bout, and the rate of change (heating or cooling) of degree·min^{-1} to be considered a departure or return.

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These three parameters were estimated from a sample of 15 data logger deployments that had simultaneous video camera data (Fig. 1). We then opened RHYTHM files in program RAVEN Pro, version 1.3 for Windows (Charif et al. 2008) to check for accuracy. From the comparison of the program RHYTHM output to the results of the simultaneous camera and data logger deployments, it became apparent that the temperature data loggers were unable to accurately document off-bouts that occurred in periods with similar ambient and nest temperatures, such as in the late morning and early evening. Additionally, they were unable to accurately provide information on departures in the middle of the day owing to greater fluctuations in ambient temperature. Because of these difficulties, we limited the data analysis to nocturnal off-bouts between sunset and the following sunrise. During this time period, we had excellent concordance (<0.25 min difference) between video data and temperature data loggers and we were confident in our ability to define departures using just data loggers at night. We obtained daily sunrise and sunset schedules for our study site for the 3 years of the study from the Astronomical Applications Department of the United States Naval Observatory.

The temperature data loggers were unable to accurately determine durations of departures of <5 min. We determined this by using PROC MIXED (SAS Institute Inc. 2006) to compare off-bouts for all 15 nights where both data loggers and video were used. The two methods did not differ in either duration or timing off-bouts >5 min ($P > 0.60$). The differences that occurred for off-bouts with durations of <5 min could have been due to any number of influences, such as the data logger missing shorter off-bouts because of the 1 min time span between temperature readings, or false-positive short departures caused by the bird's activity during incubation (turning eggs or adjusting itself over the eggs). This 5 min limitation is similar to other studies of incubation monitoring using temperature data loggers (Hoover et al. 2004). Based on this finding, we chose to include in the analysis only off-bouts >5 min in duration.

Statistical analyses

We used PROC MIXED (SAS Institute Inc. 2006) to model duration of nocturnal off-bouts from the nests of incubating Mountain Plovers while accounting for multiple contributions from individuals. In addition to sex of the tending adult, other effects included in the model set were the linear effect of nest age (day of incubation determined from a combination of egg flotation and known hatch dates; Westerskov 1950; Dinsmore et al. 2002), the year, and the linear effect of day of the sampling season. Sunrise and sunset times differed across the Mountain Plover breeding season by as much as 0.45 and 0.3 h, respectively, so we used the mid-point between these two times to determine the pattern of departures. The exact structure of this pattern was not apparent, so we included a linear, quadratic, and cubic effect of time of departure from the middle of the night in the model. We included a binary effect for days when ambient temperature was greater than 30 °C, as Mountain Plovers exhibit cooling behavior at temperatures greater than this and temperatures greater than 43 °C likely cause irreversible injury to the developing chick (Grant 1982). We also included a binary effect of measurable precipitation the previous day because incubating plovers remained on their nests during rain events (S.J. Dinsmore and P.D.B. Skrade, personal observation). Temperatures and precipitation were obtained from a NOAA weather station in the study area. We constructed a single mixed model with the pertinent fixed effects described above including the interactions of sex and season, and sex and the time from the middle of the night (linear, quadratic, and cubic effects) and with individual birds as a random effect. Effects were then examined using F tests. We chose this approach because the nesting of fixed and random effects (e.g., sex and individual) meant it was not possible to compare models of fixed and random effects when the fixed effects change with each model (Littell et al. 2006). This model assumes normality of the data and we used $\alpha = 0.05$ as the level of statistical significance for all hypothesis tests.

Results

We recorded 857 video hours and from these data we determined that males, on average, made 1.48 departures·video hour^{-1} (SE = 0.35 departures·video hour^{-1}, $n = 6$ deployments) spending, on average, 9% (SE = 5%) of the observed time off the nest. Females made 1.41 departures·h^{-1} (SE = 0.11 departures·h^{-1}, $n = 24$ deployments) and spent, on average, 10% (SE = 2%) of the observed time off the nest. Departures occurred at all hours of the day (Fig. 2). However, during the day the birds made frequent, short off-bouts, presumably to prevent the eggs from overheating in the sun; longer diurnal off-bouts generally occurred in the mornings and early evenings (Fig. 3). We logged >10 000 h of temperature data during the 2006–2008 nesting seasons. After limiting the data to off-bouts that occurred between the hours of sunset and sunrise, we found that males contributed 1925 off-bouts with a mean duration of 0.38 h (SE = 0.01 h), whereas females contributed 2716 off-bouts with a mean duration of 0.36 h (SE = 0.01 h). The initial mixed model found the interactions of sex with the day of season and the linear, quadratic, or cubic time of nocturnal off-bout were not significant (Table 1), and so we ran the model again with the interactions removed. From this model, we found no significant difference in the duration of off-bouts of male and female Mountain Plovers (type III test for fixed effects (MIXED): $F_{[1,103]} = 0.36$, $P = 0.55$).

There was no difference in the duration of nocturnal off-bouts throughout the incubation period ($F_{[1,4527]} = 1.11$, $P = 0.29$) and the duration of nocturnal off-bouts did not differ across years ($F_{[2,4527]} = 1.77$, $P = 0.17$). Whereas the linear time trend did not have a significant effect on duration of off-bouts within a night ($F_{[1,4527]} = 0.02$, $P = 0.88$), the quadratic ($F_{[1,4527]} = 82.73$, $P < 0.01$) and cubic ($F_{[1,4527]} = 5.94$, $P = 0.02$) time trends of nocturnal off-bout were significant and showed a pattern of longer off-bouts early and in the middle of the night (Fig. 4). However, we found that incubating Mountain Plovers made longer nocturnal off-bouts earlier in the breeding season (Fig. 4; $F_{[1,4527]} = 9.65$, $P < 0.01$). Ambient temperatures warmer than 30 °C had no effect on the duration of nocturnal off-bouts ($F_{[1,4527]} = 1.22$, $P = 0.27$); however, if there was measureable precipitation that day, incubating Mountain Plovers made significantly longer nocturnal off-bouts (Fig. 5; $F_{[1,4527]} = 4.55$, $P = 0.03$).

Fig. 1. Characteristic nest temperature trace (°C) of the nocturnal incubation behavior of Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, USA, during 22–23 July 2007. Temperatures were recorded every minute using a data logger placed in the nest, while departure and return times were determined from simultaneous remote video observation.

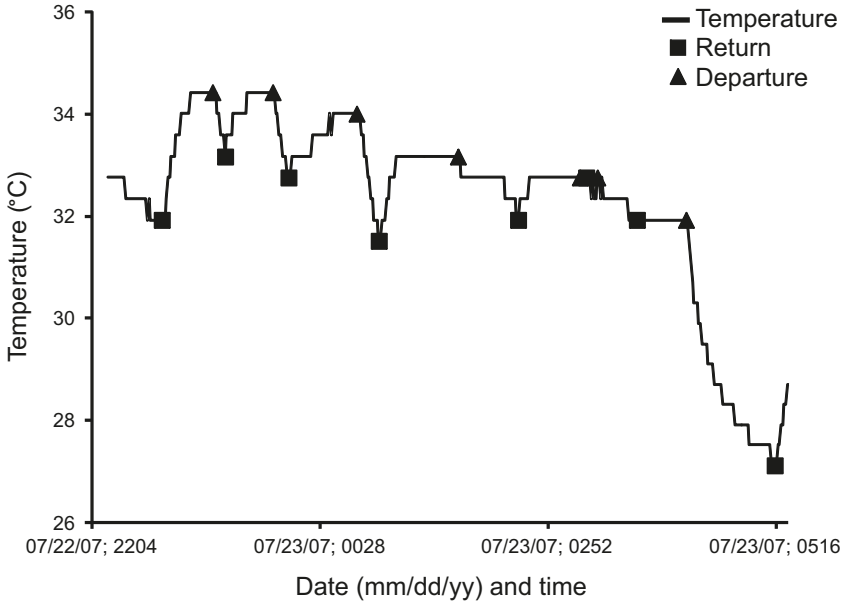
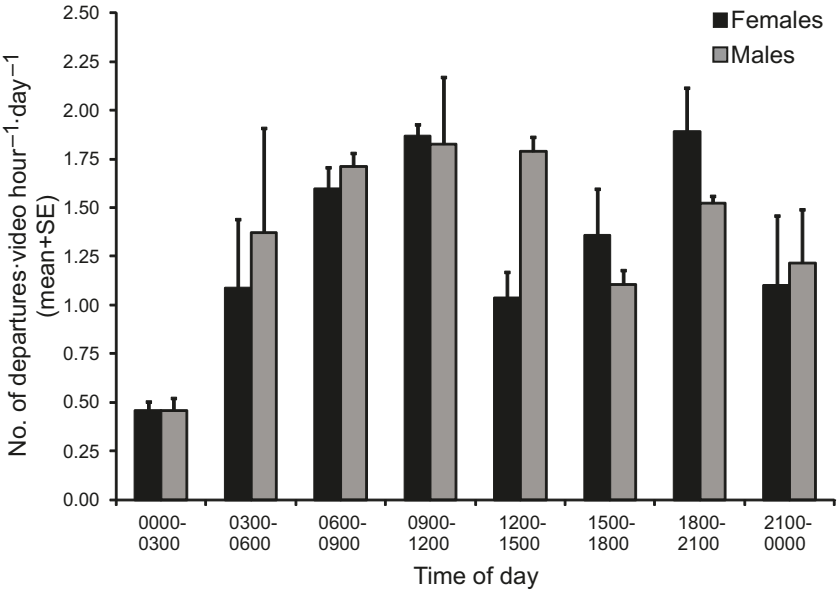


Fig. 2. Number of departures from the nest·video hour^{-1}·day^{-1} (mean + SE) by 6 male and 24 female Mountain Plovers (*Charadrius montanus*) observed in Phillips County, Montana, USA, during 2007. Time of day references the hour on a 24 h clock.



Discussion

The time of night that a Mountain Plover departs from its nest clearly plays an important role in the duration of its off-bout. From the small sample of video data, we documented 13 occasions when incubating Mountain Plovers left the nest after sunset and were visibly feeding within the limited scope of the camera. These observations, combined with the activity of this species' prey, could explain the longer off-bouts early and in the middle of the night. Mountain Plovers are insectivorous and insects in the orders Orthoptera and Coleoptera make up a large part of their diet (Baldwin 1971). Crickets (Burpee and Sakaluk 1993), ground beetles (Ottesen 1985; Lövei and Sunderland 1996), and darkling beetles (Parmenter et al. 1989) are all active at night and are known food items of the Mountain Plover (Knopf 1998). Carabid beetles are more active at midnight during the summer months in northern latitudes (Ottesen 1985) and breeding crickets show a similar pattern (French and Cade 1987). A study of nocturnal foraging behavior in breeding Piping Plovers (*Charadrius melodus* Ord, 1824) showed that foraging rates were considerably lower than during the day (Staine and Burger 1994). This could cause the bird to spend longer away from the nest to obtain the same amount of food.

Mountain Plovers occasionally give mating calls at night (S.J. Dinsmore and P.D.B. Skrade, personal observation) and

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Fig. 3. Duration of off-bout (raw h; mean + SE) from the nest by 6 male and 24 female incubating Mountain Plovers (*Charadrius montanus*) observed using a remote video recorder in Phillips County, Montana, USA, during 2007. The apparent decrease in length of off-bouts for females and increase in length of off-bouts for males were severely biased by one female that left its nest on three different days at ~2100 and was gone for 3–5 h and one male that left its nest at 0130 and did not return for over 3.5 h. Time of day references the hour on a 24 h clock.

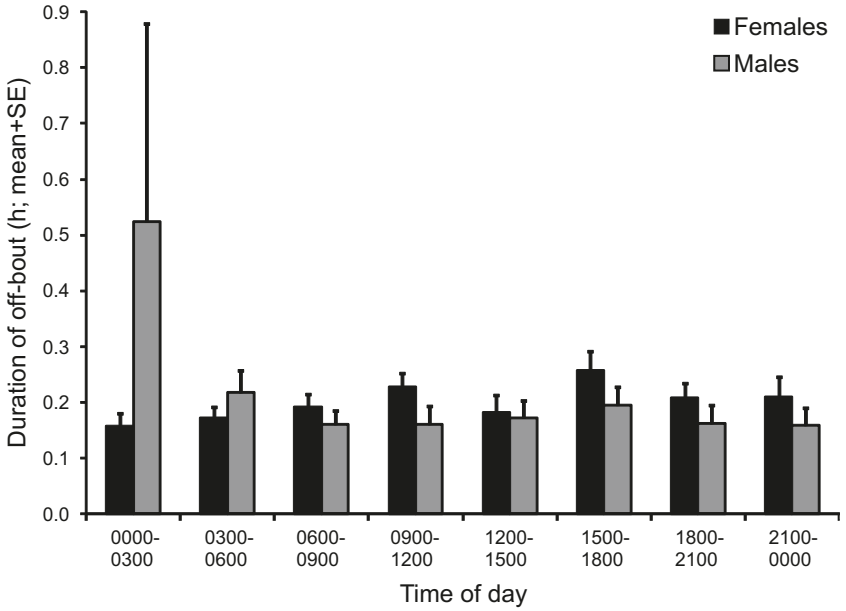

Table 1. Mixed model analysis of duration of nocturnal off-bouts of incubating Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, USA, during 2006–2008.

Effect	Estimate	df	SE	*P*
Intercept	0.532	103	0.059	<0.001
Rain	0.035	4523	0.017	0.039
Sex (male)	0.109	103	0.058	0.063
Age	–0.002	4523	0.001	0.213
Season	–0.002	4523	0.001	0.002
Season × sex (male)	–0.002	4523	0.001	0.144
Year (2006)	–0.056	4523	0.037	0.129
Year (2007)	–0.025	4523	0.027	0.371
Temperature (cool)	–0.021	4523	0.020	0.288
Time from middle of night	0.010	4523	0.008	0.219
Time from middle of night^2	–0.010	4523	0.002	<0.001
Time from middle of night^3	–0.002	4523	0.001	0.007
Time from middle of night × sex (male)	–0.018	4523	0.013	0.171
Time from middle of night^2 × sex (male)	–0.004	4523	0.002	0.139
Time from middle of night^3 × sex (male)	0.001	4523	0.001	0.229

Note: "Rain" indicates that there was measurable precipitation the previous day; "sex" refers to the gender of the incubating adult; "age" is the day since the onset of incubation; "season" refers to the Julian day of the breeding season; "temperature" is a categorical "warm" or "cool" referring to days where the maximum ambient temperature did or did not exceed 30 °C. "Time from middle of night" refers to the time (h) from the midpoint between sunset and the following sunrise.

other shorebirds perform breeding activities after sunset (Johnson et al. 2002, 2003). As a result, the observed off-bouts could potentially be a response to conspecifics, either for courtship or as agonistic behavior, and the seasonal decrease in these behaviors could explain the observed pattern of shorter off-bouts later in the season. Low numbers (n < 5) of both of these interactions were documented with nocturnal video recordings, which is of note because of the limited range of vision of the camera. Additionally, seasonal increases in the abundance of the previously mentioned prey species could help explain the decrease in duration of off-bouts later in the breeding season (Olson 1985; O'Meilia et al. 1982). Increases in food availability allow for shorter off-bouts because foraging Mountain Plovers may encounter nocturnal insects more frequently (Eikenaar et al. 2003).

Our results suggest that male and female Mountain Plovers have similar nocturnal incubation behaviors. Both sexes have similar physical demands during incubation and are not sexually size dimorphic (Iko et al. 2004; Lislevand and Thomas 2006), so this result is not completely unexpected. To compensate for the energetic stress of egg-laying, female Mountain Plovers may delay incubation (Knopf and Wunder 2006)

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Fig. 4. Duration of nocturnal off-bouts (raw h; mean ± SE) in relation to the mid-time between sunset and sunrise and the day of season for nesting Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, USA, during 2006–2008. "Early" and "late" refer to two 25-day periods during the field season.

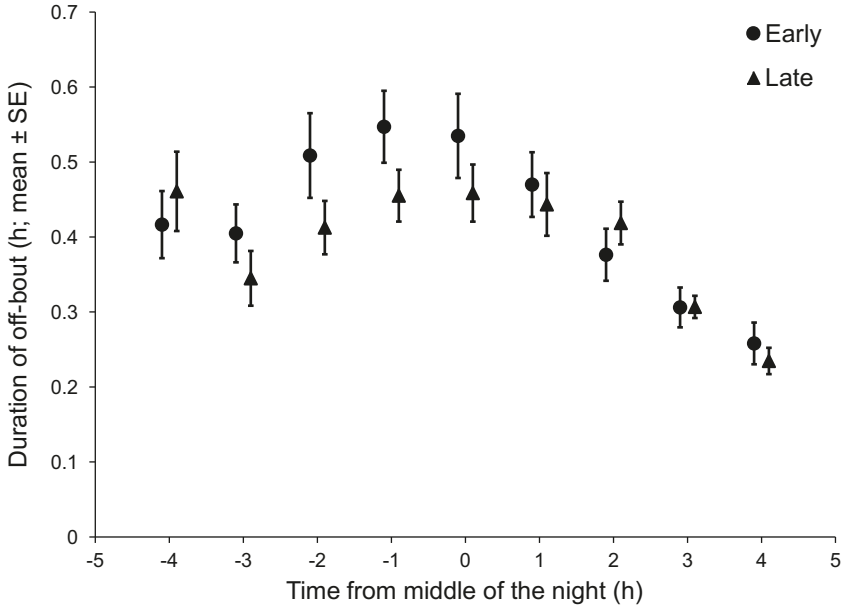
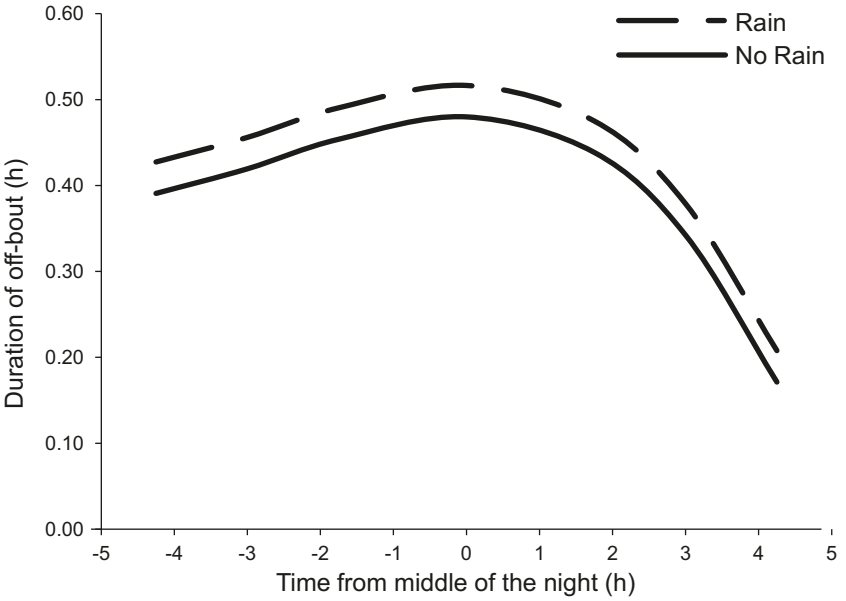


Fig. 5. Model-estimated lengths of nocturnal off-bouts (h) in relation to the mid-time between sunset and sunrise for nesting Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, USA, during 2006–2008. Estimates were produced for 30 June, the approximate mid-point of the breeding season, to model differences in off-bouts following measurable precipitation.



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to improve their condition and reduce the need to leave the nest to forage. Another possible reason for a lack of behavioral differences between the sexes of this species might be because of their reduced clutch size. In the majority of Charadriidae, the typical clutch size is four eggs (Maclean 1972) compared with three in Mountain Plovers (Knopf and Wunder 2006). Increases in clutch size require increases in the energetic cost of incubation (Thomson et al. 1998) and so perhaps the reduced clutch is also to reduce the energetic costs for uniparental incubation. Lastly, Mountain Plover nests tended by males or females appear to have differential survival (Dinsmore et al. 2002), and we initially expected to find sex-related differences in incubation patterns. The absence of such patterns may have resulted from seasonal differences (male-tended nests are earlier than female-tended nests), or from some other unknown cause.

Although there have been many studies of nest attendance in birds, few can be practically applied to open-cup ground-nesting shorebirds. Direct observation and video monitoring require a large time commitment and may have a high monetary cost for equipment. Other methods can cause major disturbance at the nest through removal of nest contents

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(Kosztolányi and Székely 2002) or destruction of an egg to implant a thermocouple. These are not feasible when working with a species of conservation concern. Although the data loggers used in this study were unable to accurately measure nest attentiveness at all hours of the day, the method was unobtrusive, inexpensive, and provided valuable information about the nocturnal activities of this species.

Recordings of nest or egg temperature of cavity- or cup-nesting birds often clearly show adult incubation activity (Vleck 1981; Voss et al. 2008), but the resolution at which arrivals and off-bouts from the nest can be determined in open-cup ground-nesting shorebirds is harder to ascertain. One study of ground-nesting shorebirds in Siberia (Tulp and Schekkerman 2006) was successful in measuring activity using temperature data loggers because the ambient temperature was always lower than the nest temperature; a similar study of Piping Plovers in Massachusetts, USA, was unable to accurately estimate nest attendance (Schneider and McWilliams 2007). Although use of this type of data logger was minimally invasive, it was unable to accurately delineate nest activity during a large portion of the day. Many factors can influence the accuracy of these data loggers, but the most important appear to be occasions when (*i*) ambient and nest temperatures are similar and the logger simply does not recognize off-bouts, or (*ii*) ambient temperatures are greater than nest temperatures and the temperature data are no longer interpretable. Other factors that might influence the results of the data logger include occasional direct contact with the brood patch or the ability of the eggs to retain heat.

Future research should examine the body condition of Mountain Plovers throughout incubation and relate this to incubation activity. A study of Eurasian Dotterels (*Charadrius morinellus* L., 1758), a close relative of the Mountain Plover, showed that body mass of incubating males decreased during the time period when they were the sole incubator, but in cases where the incubation duties were shared with females, the mass of those males was 7% greater than that of the uniparental males (Holt et al. 2002). Dotterels are forced to expend greater energy warming their eggs in a cooler climate than Mountain Plovers, but they are still constrained to their nest, similar to Mountain Plovers, at times when air temperatures are >30 °C. Instead of expending energy warming their eggs, Mountain Plovers must pant and gular flutter while shading their eggs. These activities are also physically demanding, and when combined with an inability to forage because of possible egg overheating, we expected that incubating adults would have longer nocturnal off-bouts following hot days. We did not find a strong ambient temperature effect in this study, which suggests that the physical demands of incubation during hotter days are not different than on cooler days, regardless of the costs of self-cooling. However, when there was measurable precipitation the previous day, incubating Mountain Plovers spent significantly more time away from their nest, regardless of whether the precipitation fell during the day or night. This is similar to the findings of other studies of incubation behavior that found open-nesting incubating birds become more attentive when it rains (Skutch 1962). The result suggests that rainy days are energetically more costly to the incubating adult, assuming that the increased time that they are away from the nest the following night is spent feeding. This would fit with our prediction that birds attempt to recoup energy that was lost when they were constrained to the nest during the day. In general, Mountain Plovers do better during dry periods with higher annual (Dinsmore 2008) and nest survival (Dinsmore et al. 2002).

This is the first study to describe the extent of nocturnal activity during the incubation stage of a bird species with uniparental care by both sexes. Although it was not possible to provide a connection between incubation activity and nest survival because of the study design, we did find that there was very little difference between male and female investment during incubation. Additionally, our study of Mountain Plover incubation behavior can be incorporated into future management of this uncommon species. Our results illustrate that the Mountain Plover is most active in the middle of the night and that nocturnal activity declines throughout the incubation period. Understanding the relationship between the time of nocturnal off-bouts and the incubation stage has implications for mitigating disturbance to nests during potentially sensitive periods and may ultimately be used to benefit conservation efforts for this species.

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