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Egg-Size Investment in a Bird with Uniparental Incubation by Both Sexes

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Abstract

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Keywords

Charadrius montanus, egg size, maternal investment, Mountain Plover, uniparental care

Disciplines

Developmental Biology | Natural Resources Management and Policy | Ornithology | Population Biology | Poultry or Avian Science

Comments

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EGG-SIZE INVESTMENT IN A BIRD WITH UNIPARENTAL INCUBATION BY BOTH SEXES

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Abstract. The Mountain Plover (*Charadrius montanus*) has an uncommon parental care system in which males and females tend separate nests. To improve their fitness in this system, females have the opportunity to allocate their reproductive investment to male-tended nests and their own nests differently. To examine investment we measured dimensions of plover eggs in Phillips County, Montana, and calculated their volumes. We modeled possible differences in egg volume in male- and female-incubated nests in relation to the effects of sex of the incubating adult, Julian day of nest initiation, and drought conditions. We measured >1000 eggs from 194 nests tended by 131 females and from 213 nests of 148 males. Male- and female-incubated eggs had similar mean volumes (13.20 versus 13.17 cm³, respectively) but differed significantly across the breeding season. The eggs in female-incubated nests tended to be larger than those in male-incubated nests early in the breeding season but were smaller as the season progressed, while the volume of male-incubated eggs peaked in the middle of the season. Egg volumes were affected by drought conditions, being larger during the driest periods of this study. Volumes within a nest were similar and were not influenced by the age of the incubating adult. Larger eggs tended to produce larger chicks. The similarity in the size of Mountain Plover eggs, even between male- and female-incubated nests and under different environmental conditions, provides evidence for stability of this uncommon system of parental care.

Key words: *Charadrius montanus*, egg size, maternal investment, Mountain Plover, uniparental care.

Inversión en el Tamaño del Huevo en un Ave con Incubación Uniparental por Ambos Sexos

Resumen. *Charadrius montanus* tiene un sistema poco común de cuidado parental en el cual los machos y las hembras tienden a separar los nidos. Para mejorar su desempeño biológico en este sistema, las hembras tienen la oportunidad de asignar diferencialmente su inversión reproductiva a nidos atendidos por machos y a sus propios nidos. Para examinar la inversión, medimos las dimensiones de los huevos de *C. montanus* en el Condado Phillips, Montana, y calculamos sus volúmenes. Modelamos las posibles diferencias en el volumen del huevo en nidos incubados por machos y hembras con relación a los efectos del sexo del adulto incubando, día juliano de inicio del nido y condiciones de sequía. Medimos >1000 huevos provenientes de 194 nidos atendidos por 131 hembras y de 213 nidos de 148 machos. Los huevos incubados por machos y hembras tuvieron volúmenes medios similares (13.20 vs. 13.17 cm³, respectivamente), pero difirieron significativamente a lo largo de la estación reproductiva. Los huevos en nidos incubados por hembras tendieron a ser más grandes que aquellos en nidos incubados por machos a principios de la estación reproductiva, pero fueron más pequeños a medida que avanzó la estación, mientras que el volumen de los huevos incubados por machos alcanzó un máximo en el medio de la estación. Los volúmenes de los huevos estuvieron afectados por las condiciones de sequía, siendo más grandes durante los períodos más secos de este estudio. Los volúmenes dentro de un nido fueron similares y no estuvieron influenciados por la edad del adulto incubando. Huevos más grandes tendieron a producir pichones más grandes. La similitud en el tamaño de los huevos de *C. montanus*, incluso entre nidos incubados por machos y hembras y bajo diferentes condiciones ambientales, brinda evidencia de la estabilidad de este sistema poco común de cuidado parental.

INTRODUCTION

A study of life-history characteristics is a study of tradeoffs. Investment in a particular reproductive strategy, such as producing several offspring in a relatively short time, often means that some other aspect of reproduction (e.g., offspring size) will be limited (Stearns 1976). For some species, such as shorebirds, clutch size is largely constrained phylogenetically (Lack 1968, Arnold 1999), so females are often unable to increase

the number of propagules that they produce and instead invest greater resources in individual eggs. Among taxa that produce cleidoic eggs, the female must acquire all of the nutrients that the embryo requires for its growth and development prior to egg laying (Clutton-Brock 1991). Life-history theory predicts that the greater the investment per offspring the greater the increase in offspring fitness (Bernardo 1996). This is generally true in relation to maternal investment in eggs, as relatively larger eggs

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tend to produce larger offspring and the increased size often confers survival advantages on the young (Williams 1994).

In many bird species egg size is highly variable, such that within a population the largest egg is usually $\geq 50\%$ larger than the smallest and can be up to twice as large (Christians 2002). This variation usually occurs between, rather than within, clutches and females tend to lay similarly sized eggs in successive clutches (Christians 2002). However, egg size can be affected by environmental conditions such as food availability (Ramsay and Houston 1997, Bortolotti et al. 2009) and temperature (Nager and van Noordwijk 1992), although neither of these has a very large effect on egg size (Christians 2002). The age of the laying female has also been found to affect the size of her eggs; generally older birds produce larger eggs (Christians 2002).

Shorebirds (order Charadriiformes) lay eggs relatively large in relation to their body size (Rahn et al. 1975, Ross 1979). This requires a female to give up a large proportion of her body mass in a relatively short period of time, which can cause an energetic strain (Monaghan and Nager 1997). However, it will likely improve her fitness, as it has been shown in many shorebird species that larger eggs produce larger chicks (Ricklefs 1984), and in the Charadriiformes larger chick size has been linked to improved chick survival (Parsons 1970, Blomqvist et al. 1997, Dinsmore 2008).

The Mountain Plover (*Charadrius montanus*) is a shorebird of conservation concern that breeds in disturbed areas of the Great Plains and Great Basin. This species has an uncommon system of parental care in which male and female plovers tend separate nests (Graul 1975). The male sets up a territory and displays to attract a female. After mating she lays three eggs in a nest scrape and departs, leaving him to incubate the eggs and tend the chicks by himself (Graul 1975, Knopf and Wunder 2006). The female lays three more eggs at a separate location and cares for those entirely by herself. Provided that a female lays only one set of male-tended eggs prior to laying her own set of three, most female Mountain Plovers have an overall clutch size of six eggs. The clutches are thought to be laid over a relatively short time, with the female laying on alternate days for the male, initiating her own nest shortly thereafter, and then laying at the same intervals in her own nest (Knopf and Wunder 2006). However, the opportunity does exist for a female to lay more than one male-tended set of eggs before (or after) starting her own; females have been observed copulating with more than one male within a breeding season (Graul 1975) although the frequency of such polyandry has never been quantified.

The general purpose of our study was to examine the Mountain Plover's egg size in relation to several factors. We sought to model egg volume in relation to (1) sex of the incubating adult, (2) date of nest initiation, and (3) drought. We also wanted to examine the effects of eggs' sequence and age of the incubating adult on egg size and to assess the relationship between egg size and the size of the resulting chick. We predicted that eggs in earlier nests should be larger and that egg volume should decrease through the breeding season, as in

other species of shorebirds (Sandercock et al. 1999). The mean mass of the Mountain Plover is approximately 100 g, but the mean mass of its egg in its first week of incubation is $15.4 \text{ g} \pm 1.0$ (SD; Knopf and Wunder 2006). Laying several relatively large eggs in a short period has the potential to place an energetic strain on the female (Monaghan and Nager 1997), and the result of this may be a decrease in egg size through time (Bortolotti et al. 2009). In some species egg volume has been linked to diet (Bortolotti et al. 2009), such that birds that nest in areas with more food lay larger eggs. Over the five years of this study weather conditions varied, 2006 and 2008 being drier than the historical averages, 2009 and 2010 similar to the historical average, and 2007 wetter than the historical average (Montana Natural Resource Information System 2012), which can have a large effect on the abundance and composition of the Mountain Plover's prey (Jonas and Joern 2007). The sequence in which the eggs in a clutch are laid can also influence their size (Arnold 1991, Lislevand et al. 2005), with the general pattern being one of decline. With only three eggs per Mountain Plover nest we did not predict a great difference in egg volume within a nest.

METHODS

STUDY AREA AND FIELD DATA COLLECTION

During the summers of 2006–2010 we studied Mountain Plovers breeding in an approximately 3000-km² area in southern Phillips County in north-central Montana (47° 40'–47° 55' N, 107° 35'–108° 30' W), described in detail by Dinsmore et al. (2002). Field work began in mid-May and continued until the end of the birds' breeding season, usually late July or early August. Nest searching and monitoring and the capture, handling, and banding techniques were similar each year and followed those described by Dinsmore et al. (2002). We individually color-banded adult and hatch-year birds, although we were unable to determine the age of individuals banded as adults. The Mountain Plover is sexually monomorphic (Iko et al. 2004), and we sexed the birds molecularly from feather or blood samples (Avian Biotech International, Tallahassee, FL), using techniques outlined in Dinsmore et al. (2002). This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol number 5-06-6129-Q.

At each nest we used dial calipers to measure (to the nearest 0.01 mm) the maximum length and width of all eggs. We calculated egg volume by an equation previously used for the Semipalmated Plover (*C. semipalmatus*, Nol et al. 1997), a closely related species, as

$$\text{volume} = [0.4482 \times \text{egg length} \times \text{egg width}^2] - 0.269 / 1000$$

Although the dimensions of Semipalmated and Mountain plover eggs differ slightly, this equation was the most taxonomically appropriate from the previously published equations for estimating the volume of shorebird eggs from length and width measurements (Väisänen 1977).

We determined the age of the nest and the onset of incubation by egg floatation (Westerskov 1950, Dinsmore et al. 2002). To examine the effect of season we set the earliest calendar day of nest initiation as day 1 and scaled all other initiation dates from this point (day 1 = 30 April). We assigned each nest a categorical drought condition based on the water supply and moisture status for the month of nest initiation (Montana Natural Resource Information System 2012).

We found most Mountain Plover nests after the onset of incubation so could not determine which female had laid eggs in a male-incubated nest and found it difficult to examine the effects of sequence of laying on egg size. However, in 18 nests discovered during the laying stage we marked the eggs with a nontoxic permanent marker so that subsequent eggs could be distinguished. We attempted to capture all chicks within a brood <24 hr after hatching to examine the relationship between mean egg volume (cm^3) and mean mass of the resulting chick (to the nearest 0.1 g) within a brood.

STATISTICAL ANALYSES

We used the procedure MIXED in SAS (version 9.1; SAS Institute, Cary, NC) to compare the volume of eggs in male- and female-tended nests while accounting for multiple contributions from individuals and multiple measurements per nest. To do this we constructed a single mixed model with the random effects of individual bird and nest and the fixed effects of sex of the tending adult, drought, linear and quadratic day of nest initiation, and the interaction between sex and both linear and quadratic day of nest initiation because a plot of the data suggested that this interaction might be significant. We used all-subsets model selection on the covariates to determine which model was best supported. 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 in those models changed. We also used the mixed model to examine the variability in egg size within and between individuals and nests and tested whether the variability was different from zero with z -tests. To test if the variability in egg size differed by month when a nest was initiated during a drought or not we used Levene's test for homogeneity of variance, and we used $\alpha = 0.05$ as the level of statistical significance for tests of all hypotheses.

To examine the relationship between egg size and the resulting chick's size we performed a simple linear regression of the mean volume (cm^3) of the eggs in each nest compared to the mean mass (g) of chicks in the resulting brood. We calculated the slope of this relationship and tested to see if it differed from zero ($\alpha = 0.05$).

RESULTS

During the five breeding seasons we found 194 nests of 131 female Mountain Plovers and 213 nests of 148 males, and we measured 567 and 620 eggs from these, respectively. The mean date of nest initiation was 1 June (SE = 0.7 days), 28 May (SE =

1.1 days) for males and 5 June (SE = 1.3 days) for females. Mean lengths and widths of all eggs combined were 37.23 mm (SE = 0.04) and 28.10 mm (SE = 0.02), respectively. Male-incubated eggs tended to be longer than female-incubated eggs (mean = 37.30 mm, SE = 0.05, compared to 37.15 mm, SE = 0.05), whereas female-incubated eggs were slightly wider (mean = 28.11 mm, SE = 0.03, compared to 28.08 mm, SE = 0.03), although neither of these differences was significant (type III test for fixed effects [proc MIXED]: $F_{1,261} = 2.5$, $P = 0.12$ and $F_{1,261} = 0.8$, $P = 0.36$, respectively).

The volume of male-incubated eggs was statistically different than that of female-incubated eggs (mean volume = 13.20 cm^3 , SE = 0.03, compared to 13.17 cm^3 , SE = 0.04; $F_{1,278} = 4.6$, $P = 0.03$); however, this difference is likely due to the large number of eggs sampled and is negligible in a biological sense. The eggs' size tended to vary through the breeding season, being larger in female-tended nests initiated early in the season (Fig. 1; linear and quadratic day of nest initiation, $F_{1,780} = 5.5$, $P = 0.02$, and $F_{1,780} = 5.8$, $P = 0.02$, respectively) and larger in male-incubated nests as the breeding season progressed (Fig. 2; interaction of sex of the tending adult with linear and quadratic day of nest initiation, $F_{1,780} = 4.5$, $P = 0.03$, and $F_{1,780} = 3.8$, $P = 0.05$, respectively). Drought had a significant effect on egg volume, with the largest eggs laid during the driest conditions of this study (Fig. 2, Table 1; $F_{3,780} = 3.1$, $P = 0.03$). The variability in egg size between individuals (covariance estimate = 0.27) and the variability between nests (covariance estimate = 0.27) were similar. Both were close to double the variability within a nest (covariance estimate = 0.16), and all these values were significantly different from zero (P for all z -tests < 0.0001). Similarly, the variability in egg size was more homogeneous between months experiencing drought conditions than between those that were not (ANOVA, $F_{1,1185} = 0.3$, $P = 0.60$).

In the 18 nests discovered during laying we found no difference between the volume of eggs laid first, second, or third (ANOVA, $F_{2,15} = 0.6$, $P = 0.59$, JMP statistical package, version 9; SAS Institute, Cary, NC). Only three eggs were unquestionably laid second, as we revisited nests with incomplete clutches rarely during laying.

We found 26 nests of 17 female and 28 nests of 19 male Mountain Plovers that were banded as juveniles and returned to the study area as adults. In this sample of birds of known age, there was no clear pattern of age of the tending adult influencing maternal investment in egg volume (Fig. 3). The eggs of nests tended by one-year-old males and females appeared the least similar to each other, although there was considerable variability in mean egg volume between the different age categories and we did not have any females in our oldest age categories.

During the five years of the study we were able to capture and weigh chicks from 63 broods <24 hr after hatching. Although variability in chick mass and egg volume was fairly large, there was a strong positive relationship between mean chick mass and nests with greater mean egg volumes (Fig. 4, $R^2 = 0.26$, $P < 0.01$).

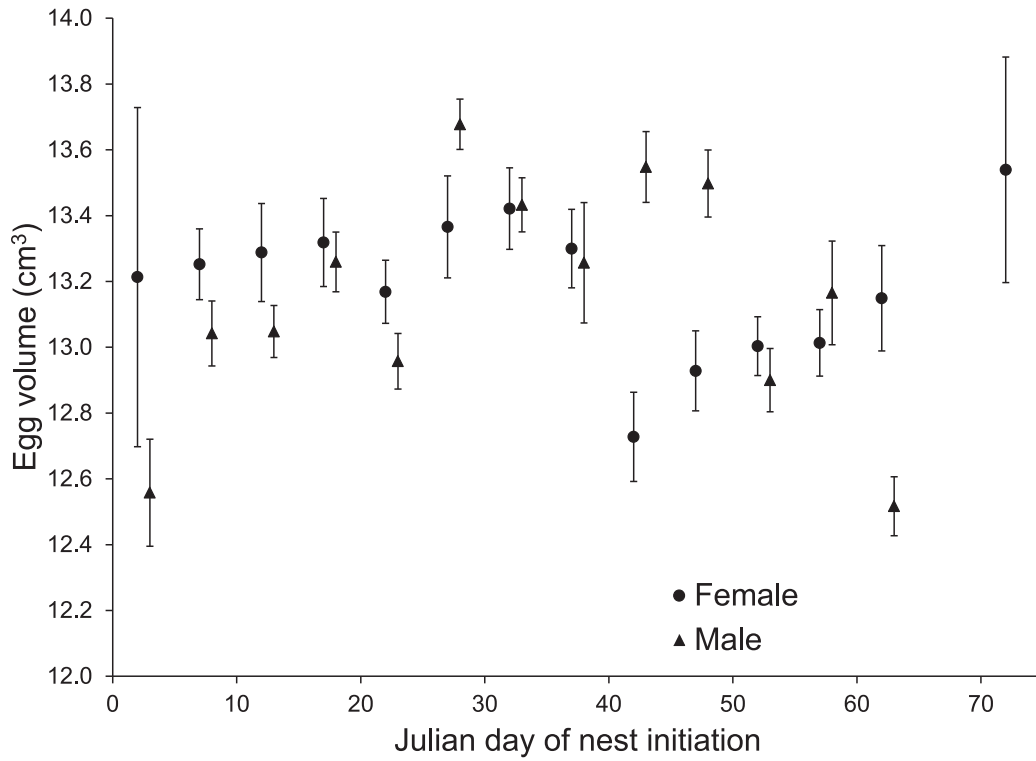


FIGURE 1. Plot of five-day means (\pm SE) of calculated egg volume (cm^3) of clutches tended by male and female Mountain Plovers in relation to Julian day of nest initiation (day 1 = 30 April) in Phillips County, Montana, 2006–2010.

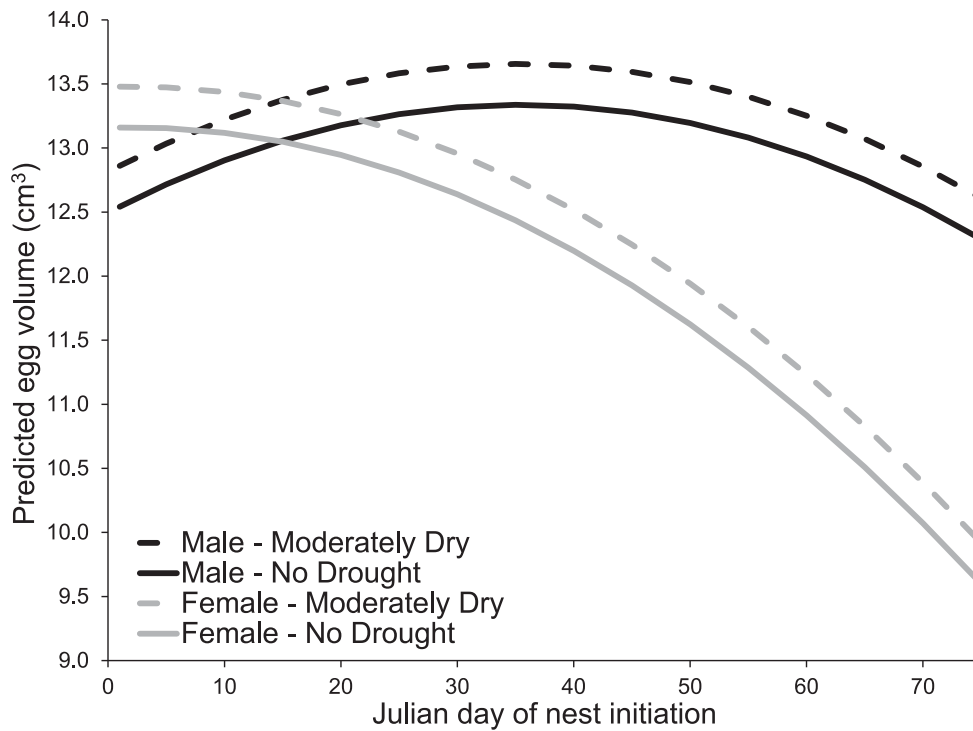


FIGURE 2. Model-estimated volume (cm^3) of Mountain Plover eggs incubated by males and females in relation to the day of nest initiation (day 1 = 30 April) and moderate drought conditions, Phillips County, Montana, 2006–2010.

TABLE 1. Mixed-model analysis of volume of eggs of incubating Mountain Plovers in Phillips Co., Montana, 2006–2010. Sex refers to that of the incubating adult, Moderately dry, slightly dry, and moist are moisture conditions, and initiation refers to the Julian day of nest initiation.

Effect	Estimate	df	SE	P
Intercept	12.495	120	0.188	<0.001
Sex (female)	0.662	278	0.309	0.033
(Drought) moderately dry	0.319	780	0.147	0.030
(Drought) slightly dry	-0.161	780	0.118	0.171
(Drought) moist	0.153	780	0.105	0.146
Initiation	0.048	780	0.015	0.001
Initiation ²	-0.001	780	<0.001	0.003
Initiation × sex (female)	-0.045	780	0.021	0.033
Initiation ² × sex (female)	0.001	780	<0.001	0.053

DISCUSSION

While the mixed model found statistically significant differences in the patterns of Mountain Plover egg volume between nests incubated by males and females across the breeding season, the observed differences are likely a result of the large sample size and mean little biologically. The results instead show that maternal investment in egg size in this species is relatively consistent even between male- and female-incubated nests and under different environmental conditions. This type of parental care, where the pair splits a clutch that the adults incubate independently, has been argued as a step toward polyandry by reducing the energetic demands on the female (Jenni 1974, Graul

et al. 1977). The result of similar egg volumes, and therefore similar “fitness” of male- and female-tended nests, suggests that this situation of uniparental care by both members of the pair is fairly stable. The rate of success of Mountain Plover nests is relatively high in comparison to that of other ground-nesting grassland birds (Dinsmore et al. 2002), so the species’ practice of increasing the responsibilities of both parents and spreading out the risk of nest depredation (while also increasing the potential number of offspring to six) is apparently effective.

In north-central Montana Mountain Plovers nest in semiarid habitats that experience regular disturbance and droughts. The females are adapted to produce many (≥6) eggs relatively large in relation to their body size in a short time under variable environmental conditions. The five years of this study ranged from moderately dry to very moist, and these conditions likely influenced the availability and accessibility of the plover’s food. The significant positive effect of drought indicates that this species invests more into its potential fitness at a time when conditions for the incubating bird could be demanding. However, even at the opposite extreme of environmental conditions during this study, females still laid six eggs that consumed a large proportion of their body mass, more than could have come strictly from fat reserves, and so food must be available to the plovers in this area.

The volume of eggs incubated by males and females both tended to decline toward the end of the breeding season, which is consistent with other studies of shorebirds (Sandercock et al. 1999) as well as other studies of egg size and laying date (Birkhead and Nettleship 1982), but the dramatically different shapes of the predicted curves is not easily explained. One possible explanation is that females have

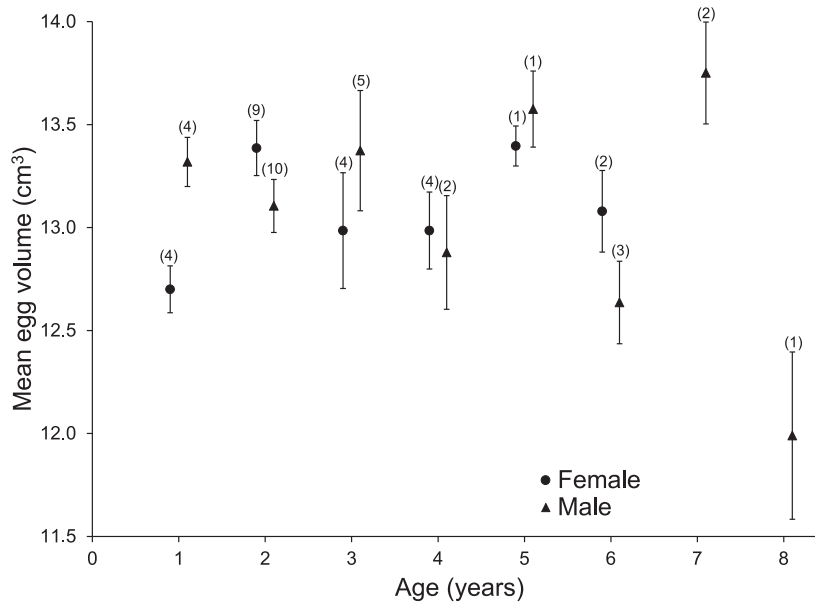


FIGURE 3. Mean (±SE) volume (cm³) of eggs tended by male and female Mountain Plovers in relation to the age (years) of the incubating adult, Phillips County, Montana, 2006–2010. The number in parentheses is the sample size.

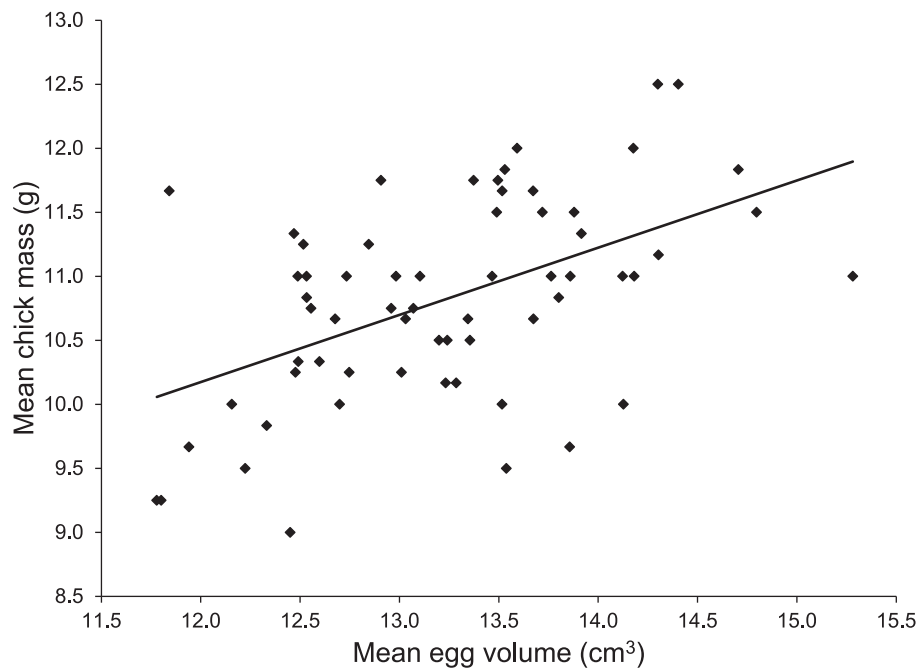


FIGURE 4. Mean mass (g) of Mountain Plover chicks within 24 hr of hatching, in relation to the mean volume (cm^3) of eggs within a clutch, Phillips County, Montana, 2006–2010.

multiple reproductive strategies (Fontaine and Martin 2006). For example, early-laying female Mountain Plovers may lay only one set of eggs for a single male and another set for themselves and forgo providing eggs for other males. Thus they are able to invest more energy into each egg than if they laid more clutches. However, if a female lays several sets of eggs for multiple males these later eggs, including the last eggs in her own set, would likely be smaller because of the energetic demand. The sex ratio of this population of Mountain Plovers is slightly biased with more males than females (1.15:1, Dinsmore and Skrade unpubl. data based on 15 seasons of birds captured at nests), which when combined with observations of females courting and copulating with multiple males (Graul 1975) suggests some polyandry and therefore that at least some females are laying eggs for multiple males.

Two other species of shorebirds have the opposite pattern in egg-size with respect to laying order. The last egg of the Northern Lapwing (*Vanellus vanellus*), a relative of the plover, is consistently smaller than the three previously laid eggs (Lislevand et al. 2005). However, one of the few shorebirds with a similar system of parental care, Temminck's Stint (*Calidris temminckii*), lays consistently larger eggs within a clutch (Väisänen et al. 1972). Like those of other species of fully precocial shorebirds, the eggs of the Mountain Plover do not appear to change with the sequence of laying (Nol and Lambert 1984, Lank et al. 1985), although to better answer this question the eggs of male-tended clutches need to be assigned to a particular female and their dimensions compared

to those she incubates herself. Examining the relationship between the physical characteristics of the female and egg size might be more informative. Reid and Boersma (1990) found that higher-quality Magellanic Penguins (*Spheniscus magellanicus*) tended to have larger eggs that provided greater fitness because of increases in early chick survival. Blomqvist et al. (1997) reported a similar result in the Northern Lapwing.

Although egg size tends to increase with the age of the female in some species (Weimerskirch 1992), this effect was not obvious in our dataset. The largest sample of known-age birds in our study were those that first returned to nest in the study area as two-year-olds, and these birds tended to lay eggs larger than those laid by females known to be one year old. One-year-old females tended to produce the smallest eggs, although there was enough overlap in the standard errors that we did not consider them to be different. While there initially appears to be a pattern of reduced egg volume in male-tended clutches, the five- and seven-year-old males tended to some of the largest eggs in this subsample. The variability in the size of eggs laid by a single individual was the same as that of eggs laid by all individuals, but because the samples were small we could not determine patterns for an individual across years. However, for age-dependent reproduction in this species to be better understood it is necessary that more individuals be followed through several years (van de Pol and Verhulst 2006).

Our study shows that in this region egg size in the Mountain Plover is fairly consistent from individual to individual, and differences between eggs laid in male- and female-tended nests across the breeding season are small. Within a nest,

eggs were of similar sizes, but further research should seek to examine the relationships between egg size and the age and physical condition of the laying female. Female Mountain Plovers tended to lay larger eggs during the driest years of this study, and maternal investment, and consequently the fitness of the offspring, may be influenced by changing environmental conditions associated with global climate change.

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LITERATURE CITED

- ARNOLD, T. W. 1991. Intraclutch variation in egg size of American Coots. *Condor* 93:19–27.
- ARNOLD, T. W. 1999. What limits clutch size in waders? *Journal of Avian Biology* 30:216–220.
- BERNARDO, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63:300–306.
- BLOMQUIST, D., O. C. JOHANSSON, AND F. GÖTMARK. 1997. Parental quality and egg size affect chick survival in a precocial bird, the Lapwing *Vanellus vanellus*. *Oecologia* 110:18–24.
- BORTOLOTTI, G. R., K. A. HOBSON, U. J. BUTT, AND P. F. SURAI. 2009. Influence of diet on egg size in American Coots (*Fulica americana*): evidence from food supplementation and biochemical markers. *Auk* 126:831–838.
- CHRISTIANS, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews* 77:1–26.
- CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, NJ.
- DINSMORE, S. J. 2008. Influence of drought on the annual survival of the Mountain Plover in Montana. *Condor* 110:45–54.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- FONTAINE, J. J., AND T. E. MARTIN. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- GRAUL, W. D. 1975. Breeding biology of the Mountain Plover. *Wilson Bulletin* 87:6–31.
- GRAUL, W. D., S. R. DERRICKSON, AND D. W. MOCK. 1977. The evolution of avian polyandry. *American Naturalist* 111:812–816.
- IKO, W. M., S. J. DINSMORE, AND F. L. KNOPF. 2004. Evaluating the use of morphometric measurements from museum specimens for sex determination in Mountain Plovers (*Charadrius montanus*). *Western North American Naturalist* 64:492–496.
- JENNI, D. A. 1974. Evolution of polyandry in birds. *American Zoologist* 14:129–144.
- JONAS, J. L., AND A. JOERN. 2007. Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: a long-term study. *Oecologia* 153:699–711.
- KNOPF, F. L., AND M. B. WUNDER. 2006. Mountain Plover (*Charadrius montanus*), no. 211. In A. Poole and F. Gill [EDS.], *The birds of North America*. Academy of Natural Sciences, Philadelphia.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LANK, D. B., L. W. ORING, AND S. J. MAXSON. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. *Ecology* 66:1513–1524.
- LISLEVAND, T., I. BYRKJEDAL, T. BORGE, AND G.-P. SÆTRE. 2005. Egg size in relation to sex of embryo, brood sex ratios and laying sequence in Northern Lapwings (*Vanellus vanellus*). *Journal of the Zoological Society of London* 267:81–87.
- MONAGHAN, P., AND R. G. NAGER. 1997. Why don't birds lay more eggs? *Trends in Ecology & Evolution* 12:270–274.
- MONTANA NATURAL RESOURCE INFORMATION SYSTEM [ONLINE]. 2012. Montana water supply and moisture conditions by county. <<http://nris.mt.gov/drought/>> (22 March 2012).
- NAGER, R. G., AND A. J. VAN NOORDWIJK. 1992. Energetic limitation in the egg-laying period of Great Tits. *Proceedings of the Royal Society of London B* 249:259–263.
- NOL, E., AND A. LAMBERT. 1984. Comparison of Killdeers, *Charadrius vociferus*, breeding in mainland and peninsular sites in southern Ontario. *Canadian Field-Naturalist* 98:7–11.
- NOL, E., M. SULLIVAN BLANKEN, AND L. FLYNN. 1997. Sources of variation in clutch size, egg size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. *Condor* 99:389–396.
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). *Nature* 228:1221–1222.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. *Auk* 92:750–765.
- RAMSAY, S. L., AND D. C. HOUSTON. 1997. Nutritional constraints on egg production in the Blue Tit: a supplementary feeding study. *Journal of Animal Ecology* 66:649–657.
- REID, W. V., AND P. D. BOERSMA. 1990. Parental quality and selection on egg size in the Magellanic Penguin. *Evolution* 44:1780–1786.
- RICKLEFS, R. E. 1984. Egg dimensions and neonatal mass of shorebirds. *Condor* 86:7–11.
- ROSS, H. A. 1979. Multiple clutches and shorebird egg and body weight. *American Naturalist* 113:618–622.
- SANDERCOCK, B. K., D. B. LANK, AND F. COOKE. 1999. Seasonal declines in the fecundity of arctic-breeding sandpipers: different tactics in two species with invariant clutch size. *Journal of Avian Biology* 30:460–468.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3–47.
- VÄISÄNEN, R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. *Annales Zoologici Fennici* 14:1–25.
- VÄISÄNEN, R. A., O. HILDÉN, M. SOIKKELI, AND S. VUOLANTO. 1972. Egg dimension variation in five wader species: the role of heredity. *Ornis Fennica* 49:25–44.
- VAN DE POL, M., AND S. VERHULST. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. *American Naturalist* 167:766–773.
- WEIMERSKIRCH, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* 64:464–473.
- WESTERSKOV, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56–67.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68:35–59.