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## THE BREEDING BIOLOGY OF THE NORTHERN PYGMY-OWL: DO THE SMALLEST OF THE SMALL HAVE AN ADVANTAGE?

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**Abstract.** We explored the breeding biology of the Northern Pygmy-Owl (*Glaucidium gnoma*) from 2007 to 2009 in a forested reserve in Portland, Oregon. Large body size is often assumed to give animals reproductive advantages, and we tested whether body size affected timing of breeding and examined variation in diet, breeding date, clutch size, and reproductive success to explore whether the presumed benefits of large body size are evident in this species. The average size of 13 clutches was 5.8, and nest success was high (92%); 22 successful nests fledged an average of 5.2 young. Dates of first laying varied over an 18- or 19-day period in each year and averaged 3 weeks earlier in 2008 than in 2009. Early breeders laid larger clutches. After the effect of breeding site was controlled for, small rather than large female pygmy-owls bred earliest. The same pattern of small size was evident in all years. Diet varied by year in regard to whether mammals (2008) or birds (2007 and 2009) were the dominant prey taken, and the owls bred earlier in 2008 occurred when mammals dominated their diet. Although small females tended to breed earlier in all years, it was only in 2009 when pairs bred very late and birds dominated their diet that small females also laid larger clutches and fledged more young. These data suggest that the merits of small or large body size may vary with stages of the breeding cycle and ecological conditions.

**Key words:** *body size, breeding biology, Glaucidium gnoma, pygmy-owl, timing of breeding.*

### Biología Reproductiva de *Glaucidium gnoma*: ¿Tiene lo Más Pequeño de lo Pequeño una Ventaja?

**Resumen.** Exploramos la biología reproductiva de *Glaucidium gnoma* desde 2007 hasta 2009 en una reserva forestada en Portland, Oregón. Usualmente se asume que el tamaño de cuerpo grande confiere a los animales ventajas reproductivas. Nosotros evaluamos si el tamaño de cuerpo afectó el periodo reproductivo y examinamos variaciones en la dieta, fecha reproductiva, tamaño de la nidada y éxito reproductivo para explorar si los presuntos beneficios del tamaño de cuerpo grande son evidentes en esta especie. El tamaño promedio de 13 nidadas fue 5.8 y el éxito de anidamiento fue alto (92%); 22 nidos exitosos empollaron un promedio de 5.2 jóvenes. En todos los años, las fechas de puesta variaron a lo largo de un periodo de 19 días y comenzaron tres semanas antes en 2008 que en 2009. Los individuos que anidaron más temprano pusieron nidadas más grandes. Luego de controlar el efecto del sitio de anidación, en general las hembras más pequeñas de *G. gnoma* anidaron más temprano. El mismo patrón de tamaño pequeño fue observado en todos los años. La dieta varió por año según si los mamíferos (2008) o las aves (2007 y 2009) fueron las presas dominantes tomadas y las lechuzas anidaron más temprano en 2008 cuando los mamíferos dominaron sus dietas. Aunque las hembras pequeñas tendieron a anidar más temprano en todos los años, fue sólo en 2009, cuando las parejas anidaron muy tarde y las aves dominaron sus dietas, que las hembras pequeñas también pusieron nidadas más grandes y emplumaron más jóvenes. Estos datos sugieren que los méritos de un tamaño pequeño o grande de cuerpo pueden variar con las etapas del ciclo reproductivo y las condiciones ecológicas.

## INTRODUCTION

The timing of birds' breeding and reproductive output are often highly dependent on food supply (reviewed in Martin 1987, Verhulst and Nilsson 2008). Food may have a particularly important influence on the reproductive biology of predators of vertebrates. Among the Strigiformes (Korpimäki 1987, Gehlbach 1994, Korpimäki and Weihl 1998, Seamans et al. 2002, LaHaye et al. 2004) and Falconiformes (Stinson 1980, Swenson 1986, Steenhof et al. 1997) the date of laying and reproductive output often vary directly with food

abundance that is driven by climatic cycles or annual variation in weather.

Within a season, the reproductive output of early breeders is often greater than that of late breeders (von Haartman 1967, Källender 1974, Lundberg 1981, Murphy 1986, Verhulst et al. 1995, reviewed in Drent 2006), so traits that favor early breeding are at a selective advantage. However, mistiming of breeding by starting too early can lead to near total reproductive failure (Seamans et al. 2002, Lint 2005). Hence strong selection for early breeding is presumably constrained by either the immediate costs of a premature start or by females'

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inability to acquire resources sufficient to bring them into breeding condition. The ability to bring a female into laying condition is likely to vary with territory quality and access to abundant food, although individual variation may also be an important factor. Larger body size and greater body mass are widely assumed to indicate high quality, presumably either because larger individuals store more of the resources used to fuel reproduction (Verhulst et al. 1995, Verhulst and Nilsson 2008) or large size yields an advantage in competition for high-quality breeding sites (Langston et al. 1990). Regardless, large size is commonly viewed as a predictor of greater fitness (Weimerskirch 1992, Wendeln 1997). However, theoretical arguments (Downhower 1984, Blanckenhorn 2000) and some empirical studies (Murphy 1986, Barbraud et al. 2000, Massemin et al. 2000, Rotella et al. 2003) suggest that small body size may sometimes yield reproductive advantages. Smaller individuals may be able to breed earlier and/or lay a larger clutch because smaller individuals can shunt more of their daily food intake into reproduction because they require less energy to meet their daily energy needs. Additionally, the merits of being small or large may vary from year to year, and smaller individuals can realize an advantage in years of low food abundance (Massemin et al. 2000). Indeed, the energetic benefits of having a small mate in years of low food abundance may be the foundation of reversed sexual size dimorphism in owls (Hakkarainen and Korpimäki 1991), and the energetic benefits of being small may outweigh the supposed benefits of being large, such as improved nest defense (Korpimäki 1986, Hakkarainen and Korpimäki 1993). For species in which males provide food to females throughout the pre-laying and nesting periods, small females may have a reproductive advantage because it may be easier for males to meet the pair's energy needs. This is most likely true of species that are relatively small and whose reproduction is supported mostly through daily food intake rather than by fat stores (Meijer et al. 1989).

The Northern Pygmy-Owl (*Glaucidium gnoma*) is a small, diurnal, cavity-nesting owl that inhabits forests of western North America. Although widely distributed, the pygmy-owl is an inconspicuous breeder, and except for the eight nests Giese and Forsman (2003) located in Washington from 1996 to 1999, knowledge of its breeding biology consists of only a smattering of temporally and geographically disconnected accounts of nests (compiled in Holt and Peterson 2000). In an attempt to provide a comprehensive account of the life history of the pygmy-owl, we documented the reproductive ecology of a population over 3 years. Our two primary objectives were to (1) document the basic natural history of this understudied owl, and (2) describe annual variation in the timing of breeding and reproductive output to explore whether the presumed benefits of large body size are evident in this species. We therefore tested whether body size affected nest initiation by year and whether the timing of breeding, clutch size, and

fledgling production varied consistently by year with body size, diet, and body mass.

## METHODS

### STUDY SITE AND POPULATION CENSUS

Our study took place in Forest Park, a 2145-ha urban park located on the northwest boundary of the city of Portland, Oregon. The roughly rectangular park, 13 km long and 1.6 km wide, is a protected, mature forest in which bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are the dominant canopy trees. The understory of shrubs, ferns, and forbs is well developed and dominated by native plants such as sword fern (*Polystichum munitum*), Oregon grape (*Mahonia aquifolium*), salal (*Gaultheria shallon*), red elderberry (*Sambucus racemosa*), vine maple (*Acer circinatum*) and Indian plum (*Oemleria cerasiformis*).

To census the park systematically and completely, we superimposed a grid of 36-ha square blocks on a map of the park, laid out survey transects, and traversed each grid block three times each year. During surveys, we broadcast and vocally mimicked male pygmy-owls' calls; we are confident we located all adult males. We found nests by detecting sex-specific contact calls, which were often made in the vicinity of the nest.

### NEST MONITORING

We recorded nest locations with a hand-held GPS unit (GPS-map 60CSx, Garmin, Inc., Olathe, KS). Nests often exceeded 6 m in height, and we used a custom-built, pole-mounted, wireless nest-cavity viewer (Huebner and Hurteau 2007) to check nest contents. We checked nests irregularly because of our desire to minimize disturbance over the lengthy incubation and nestling periods, but checks were never more than 9 days apart and were more frequent at hatching and fledging. Only one of 12 nests with information on both clutch size and number of fledged young showed a difference (five young fledged from a clutch of 6 eggs), so to estimate the clutch size of nests discovered after hatching, we used the number of nestlings at accessible nests ( $\leq 9$  m high,  $n = 9$ ), and number of recently fledged young at inaccessible ones ( $> 9$  m high,  $n = 6$ ). We determined the date of laying of the first egg by direct observation or estimated it by backdating from hatching. For nests that were inaccessible or located late in the season, we estimated the date of laying from the date of fledging by the equation laying date = fledging date - [57 + (1.5(clutch size - 1))], where 1.5 is the estimated number of days between laying of successive eggs (Proudfoot 1996) and 57 is the combined length of the incubation and nestling periods. We considered a nest successful if  $\geq 1$  owlet fledged and productivity as the number of fledged young per nest. Because the daily mortality

rate was extremely low, we did not use the Mayfield method to estimate survival. Some nests were unreachable or difficult to view even when the nest camera could be inserted, so we also located broods within one to two days after fledging to determine productivity. Pseudoreplication was not a significant concern for our estimate of clutch size because (1) turnover in the population was high, territories were usually occupied by different females in successive years, and (2) females that did use the same territory in successive years seldom used the same cavity, so the clutch size of individual females was unlikely to reflect limitation by cavity volume.

We recorded prey type from direct observations of prey eaten by adults and young rather than from analyses of prey from pellets or simply prey delivered to young at the nest. Most observations were of males delivering prey to females, and the females fed upon this prey during the courtship, laying, incubation, and nestling periods. We also observed adult and juvenile owls capturing prey for their own consumption, and adults delivered prey to young both in and out of the nest. We categorized prey as avian, mammalian, or insect.

#### CAPTURE AND BANDING

To capture adult and juvenile pygmy-owls, we used a mist net with a live mouse as a lure or by placing a mist net near the front of the nest cavity. We plucked recently fledged owlets from branches or off the ground or captured them with a pole-mounted net. We affixed a U.S. Geological Survey band to the right leg of each captured bird and measured its body mass, wing chord, culmen, tarsus, and tail lengths. We sexed adults by the presence (female) or absence (male) of a brood patch. Although we recaptured some individuals in more than one year, pseudoreplication of body size and nest-initiation date were not a significant concern because, as noted above, rates of turnover of adults within pairs was high, such that in no case were we able to confirm that both adults of a mated pair used the same site in consecutive years. Additionally, we regularly detected replacement of mates, particularly of females, in successive years. At a given site, the cavity used was often far from the previous year's cavity (Deshler 2010), further reducing concerns that data were pseudoreplicated.

#### STATISTICAL ANALYSES

Although body mass is generally a good estimator of size, the body mass of female pygmy-owls is likely to vary substantially with time since her most recent meal and with stage of the reproductive cycle. Inferring that body mass was not useful for comparisons of size among females, we instead ran a principal component analysis (PCA) to compute a body-size index from tarsus and culmen lengths. This allowed us to test for relationships between reproduction and structural body size. Loadings for tarsus and culmen length on the first principal component were both 0.701; high scores on factor 1 thus indicated large size. Among females, wing chord and

tail length were not correlated with each other or any other measure of body size ( $-0.24 \leq r \leq 0.19$  and  $P \geq 0.35$  for both measures and all comparisons), so we did not include them in the index.

To estimate the date of laying each year we used first clutches only, and for the analysis of clutch size and laying date we excluded an incomplete clutch that was depredated. We also created a variable "clutch class" to distinguish between nests where we were able to actually count eggs (clutch class 1) and nests for which we estimated clutch size from the number of young (clutch class 0).

We used analysis of variance (ANOVA), general linear models (GLM), and two-sample *t*-tests to compare adult body mass, timing of breeding, clutch size, and number of fledged young among and within years. To test for change in adult body mass over the course of the nest cycle we standardized capture dates by creating a date ("nest age") that corresponded to the time elapsed in days between the day the first egg was laid (day 1) and the date of capture of each adult. Mean date of laying differed by year (see below), so we standardized it for some analyses by subtracting the Julian date of the day before the earliest egg was laid each year from the start date of all clutches in that year. Thus day 1 was the first date of laying by any female in a given year. We also compared discrete groupings of early- (standardized laying date  $\leq$  day 7; range 1–18.5 days) and late-breeding females (standardized laying date  $>$  day 7). GLM analysis of laying date included site (i.e., territory) as a random factor and the body size index of the female as a covariate. We did similar GLM analyses of clutch size and number of fledged young, except that we included laying date as a covariate and clutch class as a fixed factor in the GLM of clutch size to account for possible loss of eggs before hatching from nests in which clutch size was not directly observed.

To examine synchrony of breeding, we calculated coefficients of variation (CV), and used 1.0 as the threshold for high variation within any factor, considering variation high if the standard deviation was greater than the mean (Hendricks and Robey 1936). We used Pearson's correlation coefficients and simple linear regressions to explore relationships between metrics of breeding and dietary composition. We obtained daily mean temperature and precipitation from the closest available (9.8 km) weather station, at the Portland International Airport ([www.weather-warehouse.com](http://www.weather-warehouse.com)), and we summarized these data into six 21-day periods beginning 11 December of the previous year and ending on 15 April. These dates encompassed the period of approximately 4 months prior to and including the start of the pygmy-owl's breeding season. Because precipitation data were not normally distributed, we  $\log_{10}$ -transformed precipitation after first adding 0.001 prior to transformation and then adding 3.0 to restore transformed values of  $-3.0$  (i.e., no precipitation) to a value of zero, thereby achieving normality. We examined annual variation in the six weather periods with analysis of variance

(ANOVA) and Tukey's HSD tests and used linear regression to analyze the annual date of laying in relation to mean precipitation and temperature for each of those periods.

Because our sample sizes were relatively small, we included the maximum possible number of cases for each type of analysis rather than selecting a fixed number of cases for all analyses. For example, for an analysis of the relationship between body size and clutch size, we used the 22 cases for which we had information on complete clutches and female size. However, for our analysis of the relationship between body size and fledged young, we necessarily omitted the two, rare, failed nests and the one case for which we did not obtain the female's body size, and so used only 19 cases. The results of some analyses closely approached, but did not reach, the usual criterion for statistical significance ( $P \leq 0.05$ ). Nevertheless, in a few cases we report results with  $0.05 < P < 0.075$  as trends of potential biological significance because (1) our samples, though relatively small, are among the largest for describing the ecology of this species and (2) the standard cutoff for significance is arbitrary (Johnson 1999). We report means and standard error ( $\bar{x} \pm SE$ ) unless otherwise indicated.

## RESULTS

### POPULATION SIZE, BANDING, AND RECAPTURE RATES

We found the nests of 5 of 12 territory holding males in 2007, all 10 territorial males in 2008, and 8 of 9 males in 2009. In total we found 24 nests (23 initial nests and one replacement nest) over the 3 years. Pygmy-Owls frequently nested at the same sites in successive years ( $n = 12$  of 15 possible instances) but reused nest cavities only occasionally ( $n = 2$ ).

We banded 17 female, 8 male, and 26 hatch-year pygmy-owls at 11 sites. During the first 2 years, we captured and banded 13 of the 14 breeding females (93%). Two of the 11 females captured in 2008 had been captured in 2007. We confirmed that two of the four females banded in 2007 had died by May 2008. In 2009, four of the six females captured on territories occupied in the prior year had not been previously banded. Recaptured banded owls (4 females, 1 male) were on their previous year's territory. No previously banded hatch-year birds were recaptured as breeders.

### LAYING, WEATHER, CLUTCH SIZE, NEST SUCCESS, AND PRODUCTIVITY

Egg laying began significantly earlier in 2008 than in both 2007 and 2009 ( $F_{2,22} = 34.1$ ,  $P < 0.01$ ; Table 1). Within a year, breeding appeared to be fairly synchronous, as the dates of laying ranged over only about 19 days within any year ( $CV < 0.07$  in all years). Annual variation in mean date of laying showed no relationship with mean precipitation and temperature for any of the 21-day weather periods ( $P = 0.08$  for mean temperature from 26 March to 15 April;  $P > 0.12$

for mean temperature and precipitation for all other periods). However, some obvious trends in the weather were consistent with trends in laying date: (1) the delayed 2009 breeding season was preceded by a colder mid-to-late December than were the 2007 and 2008 seasons ( $F_{2,60} = 6.51$ ,  $P < 0.01$ ; Tukey's HSD), and (2) the early 2008 breeding season was preceded by the period from 12 February to 4 March being warmer than in 2009 ( $F_{2,60} = 3.11$ ,  $P < 0.05$ ; Tukey's), and 2008 was dryer than 2007 ( $F_{2,60} = 4.47$ ,  $P = 0.02$ ; Tukey's HSD) during the same March period.

Of the 13 observed clutches, 5 had 6 eggs, 4 had 5 eggs, and 3 had 7 eggs; only 1 had 4 eggs. Clutches observed prior to hatching were larger than those estimated from the number of observed young ( $5.8 \pm 0.3$  vs.  $4.8 \pm 0.3$ ,  $t_{17} = -2.40$ ,  $P = 0.03$ ), and the size of observed clutches averaged larger in 2008 than 2009 ( $6.4 \pm 0.2$  vs.  $5.5 \pm 0.3$ ,  $t_9 = 2.14$ ,  $P = 0.062$ ). The difference between the years was diminished when we included nests for which clutch size was estimated from the number of young observed ( $F_{2,22} = 2.64$ ,  $P = 0.10$ ). Clutch size declined with date of laying ( $F_{1,6} = 8.378$ ,  $P = 0.03$ ,  $n = 23$ ), was independent of site ( $F_{10,2} = 0.884$ ,  $P = 0.64$ ,  $n = 23$ ), and was larger in nests in which clutch size was directly observed ( $F_{1,5} = 9.425$ ,  $P = 0.03$ ,  $n = 23$ ). There was no interaction between site and whether or not clutch size was directly observed ( $F_{4,6} = 0.673$ ,  $P = 0.49$ ,  $n = 23$ ). Multiple regression analysis of clutch size against laying date and clutch class accounted for 44% of the variation and suggested that clutch size declined seasonally at a rate of  $0.04$  eggs  $\text{day}^{-1}$  ( $SE = 0.016$ ,  $P = 0.02$ ).

At one easily accessible nest, three eggs required 29 days to hatch, and our best estimate was that incubation required 30 days ( $n = 8$  observed nests; Table 1). The nestling period averaged 27 days (Table 1), and, on average, broods left the nest over a period of  $2.3 \pm 0.2$  days ( $n = 16$  nests, range 1.5–5 days). Young fledged from 22 of 24 (92%) initial nests, and three fledglings from a replacement nest were found late in one season. The average successful nest fledged five young (Table 1). Number of fledged young was independent of site (GLM:  $F_{10,5} = 0.853$ ,  $P = 0.61$ ,  $n = 18$ ).

### FEMALE BODY SIZE AND TIMING OF BREEDING

Our GLM analysis of timing of breeding showed that early laying was associated with small body size of females ( $F_{1,8} = 7.130$ ,  $P = 0.03$ ; Fig. 1) and varied with site ( $F_{10,8} = 4.72$ ,  $P = 0.02$ ,  $n = 20$  attempted nests). Small females consistently initiated laying during the first week of the season, and larger females initiated laying during the second week (Fig. 1). Site effects were related to the consistently late start by pairs breeding in territory FL12, at which laying began during the third week of each season, an effect that appeared unrelated to a specific female because different females occupied the site each year. A multiple regression of standardized laying date against body size ( $b = 1.88 \pm 0.538$ ,  $P = 0.003$ ) and a dummy variable that distinguished between FL12 and all other nests ( $b = 11.2 \pm 1.86$ ,

TABLE 1. Productivity and chronology (mean  $\pm$  SE) of 22 successful nests of the Northern Pygmy-Owl in Forest Park, Portland, Oregon, 2007–2009.

Year	<i>n</i>	Min. clutch	Min. fledged	Laying start	Hatching start	Fledging start	Incubation (days)	Nestling (days)
2007	5	4.6 $\pm$ 0.5	4.6 $\pm$ 0.5	21 Apr $\pm$ 3.1	27 May $\pm$ 3.0	22 Jun $\pm$ 3.0	33.0 $\pm$ 0.0	26.5 $\pm$ 1.5
2008	9	5.7 $\pm$ 0.3	5.6 $\pm$ 0.3	4 Apr $\pm$ 1.4	10 May $\pm$ 1.7	6 Jun $\pm$ 1.6	29.7 $\pm$ 0.7	27.0 $\pm$ 1.0
2009	8	5.1 $\pm$ 0.4	5.1 $\pm$ 0.4	25 Apr $\pm$ 1.9	30 May $\pm$ 1.7	27 Jun $\pm$ 1.7	29.5 $\pm$ 0.5	27.3 $\pm$ 0.6
All	22	5.2 $\pm$ 0.2	5.2 $\pm$ 0.2	16 Apr $\pm$ 2.3	21 May $\pm$ 2.2	17 Jun $\pm$ 2.2	30.0 $\pm$ 0.5	27.0 $\pm$ 0.5

$P < 0.001$ ) accounted for 73% of the variation in date of laying when all nests with information on both body size and laying date ( $n = 20$ ) were included in the analysis ( $P < 0.01$ ).

We further examined the association between female body size and timing of breeding, eliminating the females consistently breeding very late at site FL12 (Fig. 1), and comparing the average body size of early (laying date  $\leq$  day 7) and late breeders (laying date  $>$  day 7). For all years combined, females breeding early were smaller than those breeding late (Table 2). Direct comparison of tarsus and culmen lengths of early and later breeders showed that both traits were shorter in early breeders (Fig. 2). By year, females breeding early in 2008 ( $n = 5$ ) appeared to be smaller ( $-1.15 \pm 0.40$ ) than late ones ( $0.43 \pm 0.6$ ,  $n = 5$ ;  $t_8 = 2.3$ ,  $P = 0.05$ ). In 2009 early-breeding females ( $-0.76 \pm 0.6$ ,  $n = 3$ ) again appeared to be smaller than late ones ( $1.06 \pm 0.4$ ,  $n = 4$ ;  $t_5 = 2.74$ ,  $P = 0.04$ ). The sample for 2007 was too small for analysis. When we included females from site FL12, early breeders were still smaller than late ones ( $-0.87 \pm 0.3$  vs.  $0.81 \pm 0.3$ ,  $t_{19} = 3.86$ ,  $P = 0.001$ ) for all three years combined.

#### CLUTCH SIZE AND TIMING OF BREEDING

For all years combined, the sizes of clutches of early ( $n = 10$ ) and late females ( $n = 11$ ) were similar ( $5.7 \pm 0.3$  vs.  $5.0 \pm 0.3$ ,

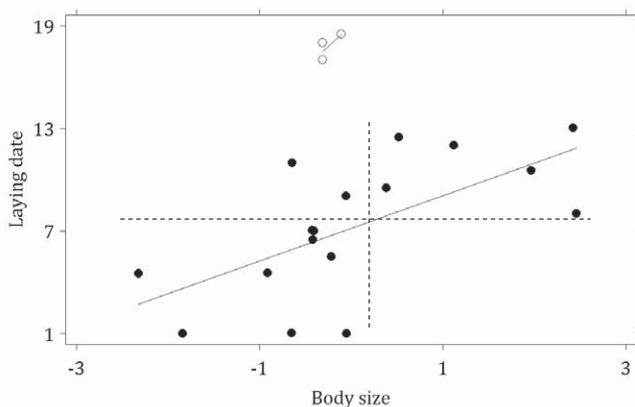


FIGURE 1. Standardized laying date (1 = start of laying in each year,  $n = 20$  nests) plotted against body-size index for female Northern Pygmy-Owls in Forest Park, Portland, Oregon 2007–2009. The plot controls for the effect of territory FL12 (unfilled circles,  $n = 3$  nests), site of latest breeding in each of the three years.

$t_{19} = -1.56$ ,  $P = 0.14$ ). In comparisons by year, in 2008, the year of greater use of mammalian prey and overall earlier breeding, early breeders did not lay larger clutches than late ones ( $6.0 \pm 0.3$  vs.  $5.6 \pm 0.5$  eggs,  $t_8 = 0.7$ ,  $P = 0.52$ ), and they fledged no more young ( $5.6 \pm 0.5$  vs.  $4.4 \pm 1.1$ ,  $t_8 = -0.97$ ,  $P = 0.36$ ). However, in 2009, a year of greater use of avian prey and overall later breeding, the smaller early-breeding females appeared to lay larger clutches ( $6.0 \pm 0.6$  vs.  $4.5 \pm 0.3$  eggs,  $t_5 = -2.54$ ,  $P = 0.052$ ), and because all eggs hatched and all young fledged, they also tended to fledge more young ( $6.0 \pm 0.6$  vs.  $4.5 \pm 0.3$ ,  $t_5 = -2.54$ ,  $P = 0.052$ ).

#### FLEDGED YOUNG AND TIMING OF BREEDING

According to our GLM of the 19 successful nests at which we had information on the female's body size (two failed nests and one without data on the female's body size omitted), the number of fledged young was independent of body size ( $F_{1,5} = 0.297$ ,  $P = 0.61$ ), date of laying ( $F_{1,6} = 0.694$ ,  $P = 0.44$ ), and site ( $F_{10,5} = 0.853$ ,  $P = 0.61$ ). However, the number of fledged young correlated negatively with the female's body size ( $n = 19$ ,  $r = -0.46$ ,  $P = 0.05$ ), suggesting that smaller females nevertheless fledged more young. So we also explored the relationship between body size and number of fledged young inter-annually by differentiating between early (laying date  $\leq$  day 7;  $n = 9$ ) and late (laying date  $>$  day 7;  $n = 10$ ) breeding, finding that early females were smaller ( $-0.77 \pm 0.26$  vs.  $0.57 \pm 0.34$ ,  $t_{17} = 3.12$ ,  $P = 0.007$ ) and tended to fledge more young ( $5.8 \pm 0.3$  vs.  $5.0 \pm 0.2$ ,  $t_{17} = -2.05$ ,  $P = 0.064$ ). Furthermore, when we considered all 22 successful nests including those without information on the female's body size, early females ( $n = 10$ ) fledged more young ( $5.7 \pm 0.3$  vs.  $4.3 \pm 0.5$ ,  $t_{20} = -2.35$ ,  $P = 0.03$ ) than late ones ( $n = 12$ ).

#### VARIATION IN BODY MASS AND DIET

The body mass of adult females ( $r = -0.45$ ,  $P = 0.06$ ,  $df = 17$ ; Fig. 3) but not that of males ( $r = 0.43$ ,  $P = 0.40$ ,  $df = 5$ ) tended to decline over the nest cycle. In 2007 and 2009 females' body mass was similar ( $75.3 \pm 2.5$  vs.  $75.5 \pm 2.6$  g; combined =  $75.4 \pm 1.7$  g,  $n = 10$ ), but in 2008 females appeared to be heavier ( $80.8 \pm 2.9$  g,  $n = 9$ ). To test for variation of body mass over the breeding cycle and by year, we combined data for 2007 and 2009 for comparison to 2008, then examined body mass in relation to nest age, using analysis of covariance with body size as a covariate. Females were heavier in 2008

TABLE 2. Comparison of body metrics (mean  $\pm$  SE) for females that bred within the first 7 days of the breeding season (i.e., early females) or later (i.e., late females) and between adult male ( $n = 8$ ) and adult female ( $n = 17$ ) Northern Pygmy-Owls captured in Forest Park, Portland, Oregon, 2007–2009.

Character	Early females	Late females	$t$ ( $P$ )	Females	Males	$t$ ( $P$ )
Body size (PC1)	$-0.77 \pm 0.26$	$1.12 \pm 0.42$	3.56 (0.003)	$0.31 \pm 0.27$	$-0.67 \pm 0.38$	2.11 (0.05)
Culmen (mm)	$13.1 \pm 0.1$	$13.7 \pm 0.2$	3.32 (0.008)	$13.4 \pm 0.1$	$12.9 \pm 0.2$	2.46 (0.03)
Mass (g)	$75.0 \pm 1.3$	$80.1 \pm 3.9$	1.37 (0.19)	$76.8 \pm 1.6$	$61.9 \pm 0.9$	6.29 (<0.001)
Tarsus (mm)	$25.9 \pm 0.4$	$27.6 \pm 0.4$	2.98 (0.01)	$26.5 \pm 0.9$	$25.9 \pm 0.4$	1.11 (0.28)
Wing chord (mm)	$93.0 \pm 0.4$	$92.8 \pm 0.2$	$-0.30$ (0.77)	$93.1 \pm 0.3$	$88.6 \pm 0.8$	6.21 (<0.001)

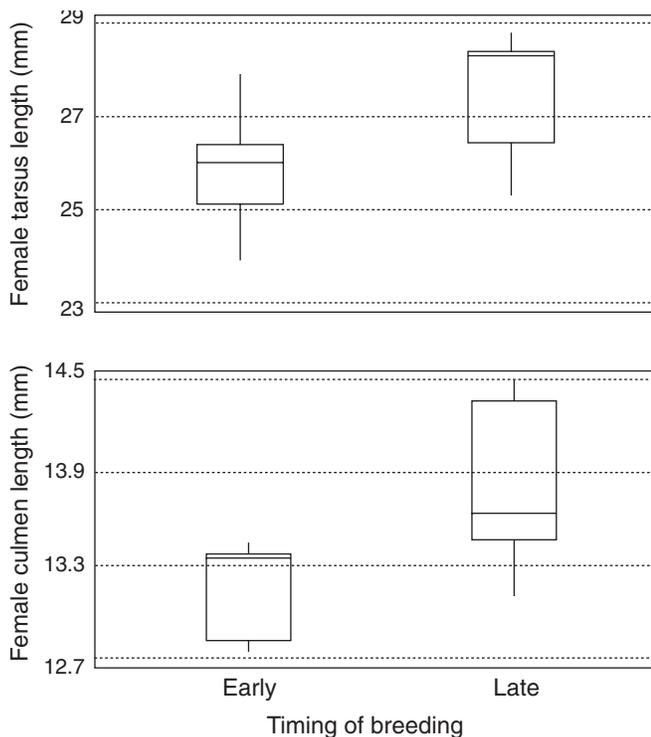


FIGURE 2. Box and whisker plots that compare tarsus and culmen lengths of early- and later-breeding female Northern Pygmy-Owls in Forest Park, Portland, Oregon, 2007–2009. Boxes enclose the middle 50% of observations, the horizontal line represents the median, and vertical lines encompass the range of observations.

( $F_{1,18} = 4.61$ ,  $P = 0.05$ ), and mass declined with nest age ( $F_{1,18} = 4.39$ ,  $P = 0.05$ ). Additionally, females were structurally larger than males and averaged 24% heavier (Table 2). Body mass had no relationship to body size for either females ( $r = 0.01$ ,  $P = 0.96$ ,  $df = 15$ ) or males ( $r = 0.26$ ,  $P = 0.51$ ,  $df = 7$ ).

Data from the three years pooled, birds and mammals contributed roughly equally to the diet (52% vs. 48%;  $n = 125$  observed prey items). However, mammals formed a greater portion of the diet in 2008 (69%,  $n = 61$ ) than in either 2007 (39%,  $n = 31$ ) or 2009 (15%,  $n = 33$ ; Fisher's exact test; 2007 vs. 2008:  $P = 0.007$ ; 2008 vs. 2009:  $P < 0.001$ ; Fig. 4). Birds constituted a larger portion of the diet in 2009 (82%) than in 2007 (61%; Fisher's exact test,  $P = 0.05$ ). Because many species of

potential avian prey were migrants that did not return before 15 April, we tested for both annual and seasonal variation in prey composition by logistic regression with prey designated as mammals (scored as 1) or birds (scored as 0; one butterfly omitted from the analysis). We found that mammals were eaten more often early in the breeding season (coefficient [ $b$ ] =  $-0.018$ ,  $SE = 0.007$ ,  $P = 0.008$ ) and more often in the first two years, especially in 2008 ( $b = -0.596$ ,  $SE = 0.264$ ,  $P = 0.02$ ).

## DISCUSSION

Pygmy-Owls in Forest Park invested heavily in reproduction during each breeding season and were highly successful in comparison to cavity-nesting raptors of similar size (Gehlbach 1994, Proudfoot 1996, Smallwood and Bird 2002). Clutches of 6 or 7 eggs were common, nestling survival was high, nest failures were rare, and offspring survival appeared to be high in the few weeks immediately following fledging. Indeed, throughout our study, pygmy-owls bred very successfully.

Mammalian prey are critically important for many temperate-zone owl species (Forsman et al. 1984, Korpimäki and Hakkaraianen 1991, Korpimäki 1992, Rohner et al. 1995, Rohner 1996), and the link between the abundance and availability of prey and reproduction has been well established for owls (Southern and Lowe 1968, Korpimäki 1986). Although we did not systematically measure the abundance of avian or mammalian prey, we recorded prey use continuously throughout each season, and from these data it appeared that mammalian prey were also particularly important for early breeding by pygmy-owls. In 2008, egg laying, which began well in advance of the arrival of many migrant birds, was significantly earlier than in the other years, and mammalian prey were taken more often than avian prey. If use reflects availability, the start 2 to 3 weeks earlier in 2008 than in the two other years may have been possible because of an abundant supply of mammalian food. In contrast, 2009 was a comparatively poor year for reproduction. In 2009, female pygmy-owls weighed less, egg laying was delayed, birds dominated the diet, and there was no seasonal shift from mammalian to avian prey as in 2008 (Deshler 2010).

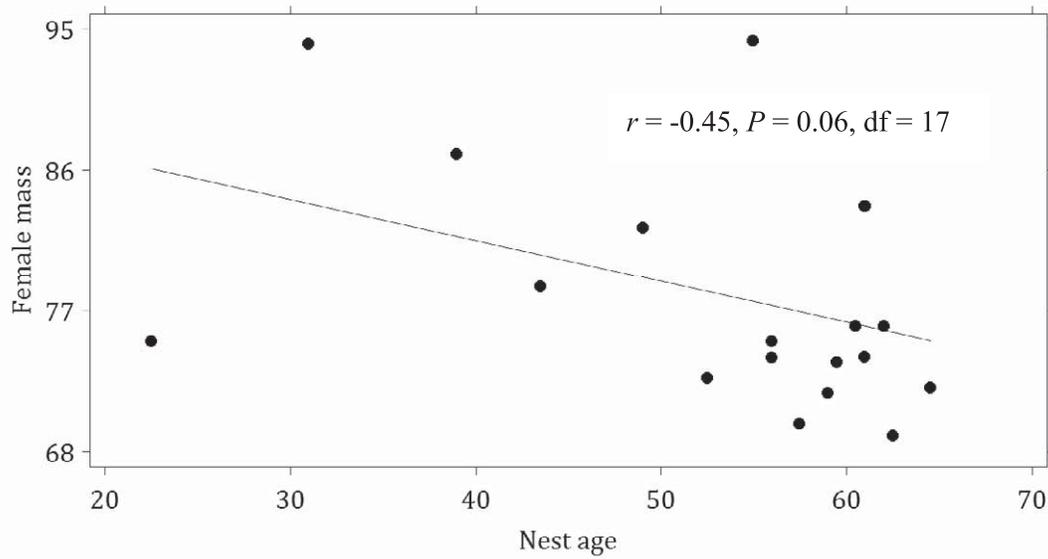


FIGURE 3. Mass of the female plotted against age of the nest for Northern Pygmy-Owls breeding in Forest Park, Portland, Oregon, 2007–2009. Nest age was computed by subtracting the start of laying (Julian date) for a given female from its date of capture, such that 1 = start of laying for each female.

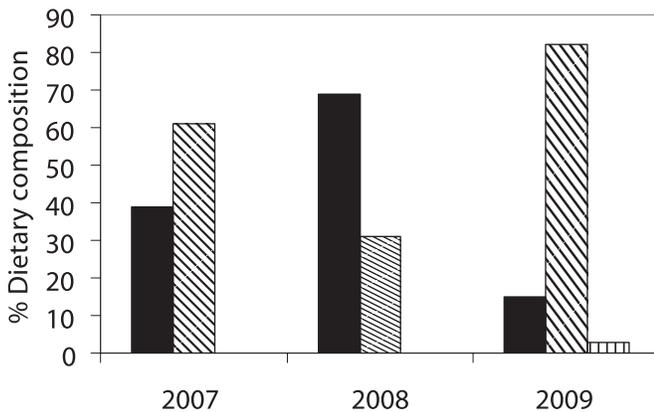


FIGURE 4. Percent dietary composition of prey, mostly delivered to the nest, for pygmy-owls on the Forest Park study area, Portland, OR 2007–2009. Prey were small mammals (black), birds (slanted lines) and insects (vertical lines).

We found that females' body mass varied with nest stage, and that fact, along with the unpredictability of a meal prior to a bird's capture and measurement, meant that body mass per se was not a reliable measure of overall size. Nonetheless, average body mass yields information on a population's condition (i.e., health) within a given year. The heavier body mass of females in 2008, the near complete reliance on mammalian prey in that year, and the success of the first documented attempt by a pygmy-owl to renest strongly suggest that 2008 was the best of the three years for this species. In contrast, 2009 was a late year in which females' body mass was low, birds dominated the diet, and both clutch size and fledgling production were below those of 2008.

#### EARLY BREEDING AND FEMALE BODY SIZE

Among the pygmy-owls we studied, small females were the first to breed. Selection for early breeding is widely recognized as important because of its association with larger clutch size (Lack 1966, Rowe et al. 1994, Sheldon et al. 2003) but also with the increased probability of renesting after failure of an initial attempt and increased likelihood of recruitment of offspring (Shutler et al. 2006, Dolan et al. 2009). We collected no information on offspring recruitment, but the clutch size of pygmy-owls at Forest Park declined seasonally, suggesting that early breeding was advantageous. Although large body size is typically associated with reproductive advantages, including early breeding (Langston et al. 1990), we and others (Murphy 1986, Barbraud et al. 2000, Massemin et al. 2000) have shown that smaller females may have an advantage in being able to be the first individuals to initiate egg production. For females, the benefit of small body size may manifest itself in the ability to shunt more food resources to reproduction rather than to maintenance. For males, small size may lead to increased aerial agility that improves efficiency of hunting and territory defense (Korpimäki 1986, Massemin et al. 2000). But whether small or large size yields an advantage may depend on annual differences in environmental conditions. For instance, Massemin et al. (2000) showed that small female Eurasian Kestrels (*Falco tinnunculus*) were able to produce more young than were larger females, but only in seasons of low or declining prey abundance. Similarly, though with a smaller sample, our data indicate that at Forest Park small female pygmy-owls bred earlier each year but achieved a reproductive advantage over large females via increased clutch and fledgling production only in 2009, a relatively poor year. And, in parallel to the conclusions of Massemin et al. (2000), the abundance of early-season mammalian prey in

2008 appeared to obviate the benefits for small females, so the absence of a difference in clutch size between early- and late-breeding pygmy-owls in that year should not have been unexpected. Thus, whether or not early breeding yields reproductive advantages for owls in general, and for smaller females in particular, may depend on the year and environmental conditions that are manifested in the abundance of mammalian prey. The apparent decline in mammalian prey in 2009 may have been caused by the harsh winter of 2008–2009, when precipitation was not unusually high but unusually cold temperatures left snow covering the ground at our site continuously for several weeks in mid-winter, an unusual occurrence in this region. Additional years of data on prey abundance, environmental conditions, and pygmy-owl reproduction are needed to fully test the hypothesis that small body size has reproductive advantages that are manifested only in years of low or declining mammalian prey abundance. But the initial years of our study suggest an intriguing interplay between evolutionary forces that sculpt the very physical structure of the Northern Pygmy-Owl.

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