

NEST ATTENDANCE BY MALE CALIFORNIA GNATCATCHERS

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Abstract.—Changes in paternal relative to maternal care either seasonally or over the nest cycle may reflect conflicting reproductive strategies between the sexes or may enhance reproductive success in the presence of sex-specific, physiological constraints. To determine whether nest attendance by males relative to females changed seasonally or with stage of the nest cycle, 107 nests of the California Gnatcatcher (*Poliioptila californica*) were monitored over the 1994 and 1995 breeding seasons, and the sex of the attending adult was noted during each visit. Relative nest attendance by the male (RNAM) was calculated by dividing the frequency of the male observed on the nest by the number of times either adult was seen on the nest. Although variability in RNAM was high, RNAM showed a decline from approximately 0.5 for first nests of the season to approximately 0.3 for late-season nests. RNAM was less during the nestling stage than during incubation or laying. During the nestling period, RNAM was less than relative nest attendance by the female, whereas prior to hatching, attendance patterns did not differ between the sexes. Because the cause of RNAM variation is unknown, future studies should aim at determining the whereabouts of gnatcatchers while off the nest.

ATENCIÓN DE NIDOS POR MACHOS DE *POLIOPTILA CALIFORNICA*

Síntesis.—Los cambios en el cuidado paternal relativo al cuidado maternal (ya sea temporal o a través del ciclo de anidaje) pueden reflejar estrategias reproductivas conflictivas entre los sexos o pueden aumentar el éxito reproductivo en presencia de limitaciones fisiológicas asociadas a un sexo. Se siguieron 107 nidos de *Poliioptila californica* durante las temporadas reproductivas de 1994 y 1995 notando el sexo del adulto interviniente durante cada visita para determinar si la atención masculina del nido (en comparación con la de las hembras) cambia estacionalmente o con las etapas del ciclo de anidamiento. La atención relativa del nido (RNAM) se calculó dividiendo la frecuencia del macho observado en el nido por el número de veces que cualquier adulto se detectó en el nido. Aunque la variabilidad en RNAM fué alta, se evidenció una reducción en RNAM de cerca de 0.5 para los primeros nidos a cerca de 0.3 para nidos tarde en la temporada. La RNAM fué menor durante el período de pichones que en los períodos de incubación o de poner. Durante el período de pichones la RNAM fué menor que la atención relativa del nido de la hembra, mientras que previo a la eclosión los patrones de atención no diferían entre los sexos. Como se desconoce la causa de la variación en RNAM, los estudios futuros debían enfocarse en determinar la localización de los individuos cuando no estén en el nido.

Few studies have examined variability in avian parental division of labor with respect to date of clutch initiation or different stages of the nest cycle (but see Buitron 1988, Fasola and Saino 1995, Guerra and Drummond 1995, and Rytönen et al. 1995). In some species, significant inequalities between male and female parental effort have evolved (Silver et al. 1985) and may reflect conflicting reproductive strategies between the sexes. For example, paternal care of the young may decrease (relative

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to the female) in the latter part of the breeding season when alternative male behavior such as promiscuity confers greater reproductive profit. Alternatively, unequal sharing in particular nesting duties may enhance reproductive success in the presence of sex-specific, physiological constraints such as laying. That is, assumption of the greater share of nest duties by the male early in the nest cycle might enable the female to prepare for or recover from the energetic demands of laying more quickly (Beissinger 1987).

I examined a form of parental care in the California Gnatcatcher (*Poiloptila californica*), a non-migratory, open-nesting passerine that lives in the coastal sage scrub ecosystem of southern California. Parental behavior in this species includes shared territory defense, nest building, incubation of the eggs, brooding of the young, and feeding of the young both as nestlings and fledglings. Beyond this, little is known about the relative roles in nest care played by males and females. I analyzed nest attendance in the California Gnatcatcher to determine whether paternal relative to maternal nest attendance varies with respect to stage in the nest cycle or date of clutch initiation.

STUDY SITE AND METHODS

This study was conducted at Miramar Naval Air Station in San Diego County, California (32°52'N, 117°05'W). The site consists of 9561 ha of elevated marine terraces and low foothills, with several extensive canyons and ridges. It ranges in elevation from 80–330 m. Dominant habitat types are chaparral and coastal sage scrub that together cover approximately 60% of the site (O'Leary et al. 1994).

Data were collected from 18 Mar.–3 Aug. 1994 and from 17 Mar.–5 Aug. 1995. These dates corresponded to the point at which the first eggs of the 1994 and 1995 breeding seasons were observed until the last known nests fledged young.

Nests were checked, on average, every 2 d from a distance of 10 m using binoculars, and the sex of the incubating or brooding adult and the time at which the observation was made were recorded. During the breeding season, the California Gnatcatcher is sexually dichromatic and can usually be sexed from a distance. However, if the sex could not be determined unequivocally or if no bird was on the nest at the beginning of the visit, the observation was not included in the analyses.

Although nest visits were usually quite brief (<30 s), the duration and frequency of observations varied depending on the purpose of the visit. Nests were visited between 0600 h and 1800 h, with the majority of visits occurring between 0700 h and 1500 h.

I calculated the relative nest attendance by the male (RNAM) for each nest by dividing the number of times the male was observed on the nest by the number of times either adult was observed on the nest. These values were then arcsine transformed prior to statistical analyses. To maximize independence of the data, RNAM values were calculated from observations of only one nest per breeding pair per year. When data were

available for multiple nests (i.e., re-nests), the nest with the most observations of either sex was used in the analyses.

To determine if RNAM varied across the nest cycle, RNAM values were calculated for each of four stages corresponding to the laying period (the first 3 d of the nest cycle starting with the laying of the first egg and continuing until the clutch is typically complete with 4 eggs; range: 2–5 eggs, $n = 40$), the first and second halves of the incubation period (each 7 d; range of total incubation: 13–16 d, $n = 22$), and the first half of the nestling period (7 d; range of total nestling period: 13–15 d, $n = 23$). Because an adult was rarely observed attending the nest during the second half of the nestling stage (see Results), observations during this period were not included in any analyses. After checking for heteroscedasticity by Levene's Test (Milliken and Johnson 1984), differences among RNAM values (dependent variable) for each of the four stages and for each year (independent variables) were determined using two-way analysis of variance.

To determine whether nest attendance by the male relative to the female varied seasonally, a single RNAM value for each nest was calculated for the period from clutch initiation to hatching as the dependent variable in an analysis of covariance. Independent variables were date of clutch initiation, year, and mean time of day during which the nest was visited. Nest loss due to predation during the nestling stage is higher early in the breeding season than later (Sockman 1997). Therefore, early in the season, a smaller percentage of nests surviving the nestling stage together with a significant change in RNAM after hatching (see Results) would bias comparisons of RNAM with respect to date of clutch initiation were observations from the nestling stage used in the analysis. Variability in RNAM explained by year ($P = 0.38$, $df = 36$) and time of day ($P = 0.21$, $df = 36$) was minimal, so RNAM was regressed on date alone. To reduce the variance among RNAM values in this analysis, only nests with at least five observations of an incubating or brooding adult were used. Applying this technique to the RNAM versus nest stage analyses was not possible since one stage was only 3 d and the others were brief (7 d).

Determining whether the first found nest of a particular pair was their first nest of the season or a re-nest would be difficult because information on the reproductive state (i.e., cloacal protuberance, presence of an edematous patch, or testis or follicular diameter) of captured individuals was not available. But all breeding pairs in this study probably initiated nesting within approximately 1 mo (mid-March to mid-April). Although nests within this first month may actually be re-nests of nests that failed very early in their cycles, nests initiated thereafter were almost certainly re-nests. Nest number as a variable is therefore subsumed by date of clutch initiation, and these two factors were statistically inseparable.

RESULTS

Overall, at least one nest from each of 107 pairs was found. But due to incomplete data on some, 62 and 37 nests were used in the RNAM versus

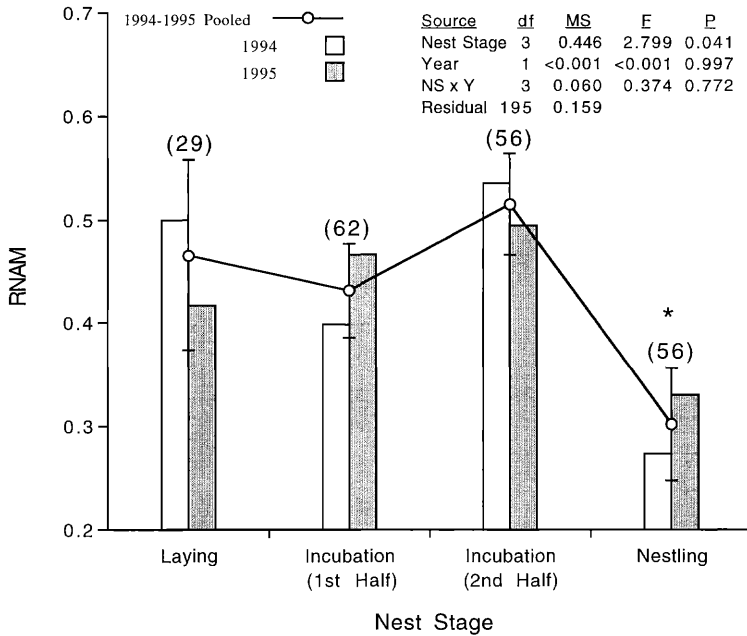


FIGURE 1. Relative nest attendance by male California Gnatcatchers (RNAM) on Miramar Naval Air Station (San Diego County, California) during four stages of the nest cycle. Standard errors and sample sizes (n) for 1994–1995 pooled data and the two-way analysis of variance table are shown. *indicates where 1994–1995 pooled RNAM values differed significantly from relative nest attendance by the female (see text for method by which this was determined).

nest stage and RNAM versus date of clutch initiation analyses, respectively. Nests were found during all stages of the nest cycle (number of nests with observations during laying = 29; first half of incubation = 62; second half of incubation = 56; first half of nestling = 56; second half of nestling = 11), but most observations of an attending adult were made during incubation or the nestling stage because these periods (each 14 d) are much longer than laying (3 d). The number of observations per nest varied from 1–12 ($\bar{x} = 5.33$).

RNAM during the first half of the nestling stage was less than that for laying or the first or second halves of incubation (Fig. 1). RNAM for individual stages did not differ significantly between years ($F_{1,195} < 0.001$, $P = 0.997$). But differences in RNAM among the four stages were greater than would be expected by chance alone ($F_{3,195} = 2.799$, $P = 0.041$). When analyzed separately by analysis of variance, pooled 1994–1995 RNAM values did not differ significantly among just the laying and incubation stages ($F_{2,144} = 0.635$, $P = 0.531$).

During laying and incubation, RNAM 95% confidence intervals (laying: 0.276–0.655; first half of incubation: 0.340–0.523; second half of incuba-

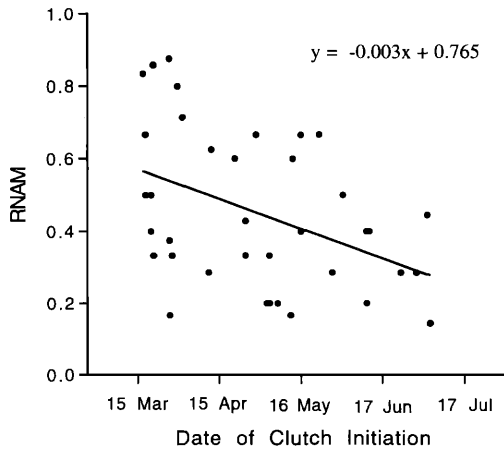


FIGURE 2. Change in relative nest attendance by male California Gnatcatchers (RNAM) with respect to date of clutch initiation.

tion: 0.418–0.613) included the value 0.5 (equal attendance by the sexes). During the nestling stage, RNAM 95% confidence intervals did not include 0.5 (0.194–0.410), indicating that, once eggs hatched, nest attendance by the male dropped significantly below nest attendance by the female (Fig. 1).

Mean RNAM estimated across the entire nest cycle was 0.419 (SE = 0.027, $n = 50$) and was significantly less than nest attendance by the female (RNAM 95% C.I. = 0.362–0.476; i.e., does not include the value 0.5). RNAM estimated from observations spanning the period from clutch initiation to hatching ($\bar{x} = 0.451$, SE = 0.035, $n = 37$) decreased significantly ($r^2 = .183$, $F_{1,35} = 7.830$, $P = 0.008$) with date of clutch initiation (Fig. 2).

DISCUSSION

Early in the nestling stage, altricial young of species such as the gnatcatcher lack substantial feather growth and cannot thermoregulate. At this time they probably require less food and more brooding than they do later in the nestling stage (Dyrz 1994, O'Conner 1984, Rosa and Murphy 1994). In a single nest visit, brooding is more likely than feeding to be observed and subsequently tallied because feeding bouts are brief relative to brooding. Therefore, during the early nestling stage, it is more likely that adults observed at the nest were brooding rather than feeding, and clearly the female assumes a greater share of brooding activity. Although the male does provide some nestling care during the first half of the nestling stage, his attendance role is less than during other periods of the nest cycle. This is consistent with other male passerines (Skutch 1957) and may be due to their typically lacking an edematous brood

patch, a development *P. californica* males also lack. Perhaps the male's role during incubation, therefore, is more protective than incubative.

I expected RNAM to be greatest early in the nest cycle, a period when emancipation from nest care would benefit a female during or having just finished an energetically costly laying period, and thereby enhance reproductive success for both sexes. Elsewhere, investigators have shown a positive correlation between female incubation effort and the length of the interval between the end of incubation and laying of a subsequent clutch (Brugger and Taborsky 1994), suggesting that incubation effort by females limits their (and therefore their mate's) reproductive output. Although RNAM during laying and the first half of incubation was greater than that during the nestling stage, during the second half of incubation, a period 7–14 d after laying, RNAM remained relatively unchanged. Females in this study laid in re-nests as quickly as 6–7 d after predation. After a post-laying period of equivalent duration, energy stores should have been replenished and RNAM have decreased accordingly. Support for my hypothesis, therefore, was weak and may be a result of laying not being as costly as expected.

The daily energetic requirements of egg laying in birds is high, approximately 29–200% of the basal metabolic rate, and daily protein requirements increase by 72–220% (Robbins 1993). Prior to such nutritionally costly events, the deposition of fat in passerines (Ricklefs 1974), possibly enabled by the female deferring more duties such as territory defense and nest building to the male (Beissinger 1987), may alleviate energetic stress in post-ovulatory females. Further, if *P. californica* males regularly bring food to incubating or laying females, a behavior observed on one occasion in this study and estimated to occur in at least 48% of avian subfamilies (Silver et al. 1985), they may assist females in protein replenishment, allowing them to forego extensive foraging in favor of incubating eggs.

Changes in RNAM according to both date of clutch initiation and nest stage, carry important implications with respect to reproductive strategies and the evolution of life history traits. For example, an unequal division in labor may evolve in mating systems where paternal nest care during particular nest stages or times of the season is maladaptive for the male. If opportunities for promiscuity are high late in the breeding season or during brood care, the time he spends in primary nest care during these times should be low (see Birkhead and Møller 1992). A link between paternal care and extra-pair-copulation opportunities remains elusive (Møller and Birkhead 1993, Smith and Montgomerie 1992), however, and no evidence to date supports such a link in the California Gnatcatcher.

Alternatively, unequal division of labor may reflect differences in male and female energy budgets imposed by costly events and may improve reproductive success. Because newly hatched nestlings require relatively little food and because the male lacks a brood patch, feeding at this time may be accomplished mostly by the male, while the female assumes brooding responsibilities. As nestlings get older, the feeding to brooding ratio

increases (Dyrzc 1994, O'Conner 1984), and the female may shift to feeding, a response typical in other species (Buitron 1988). The data herein are consistent with this scenario and may also explain why males and females were rarely observed on the nest late in the nestling stage.

Finally, the male may serve an ancillary role in nest attendance, varying his contributions as they are needed or in proportion to the female's efforts (Markman et al. 1995 and Rytönen et al. 1995). Factors such as nesting microclimate and how it changes seasonally may directly affect this (Smith and Montgomerie 1992). In fact, seasonally increasing temperatures may have caused the change in RNAM observed in this study.

My observations were made only during daylight hours. Different patterns of behavior may occur at other times, as was seen by Woods (1928), who observed in a single nest of the California Gnatcatcher that the female was primarily responsible for incubation during the night. The extent to which this pattern varies among individuals is not known. The data herein were the first to document paternal relative to maternal variation in California Gnatcatcher parental care; future studies should be directed toward determining the cause of this variation by observing the activities of gnatcatchers while off the nest.

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