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SUCCESSFUL NESTING BEHAVIOR OF PUERTO RICAN PARROTS

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ABSTRACT.—We analyzed nesting behavior of five pairs of the endangered Puerto Rican Parrot (*Amazona vittata*) during eight successful nesting attempts. Each stage of the nesting cycle (egg laying, incubation, early chick rearing, and late chick rearing) was characterized by distinct trends or levels of behavior. During egg laying, female attentiveness to the nest increased, and male attentiveness decreased. Throughout incubation and the first several days of early chick rearing, females were highly attentive to their nests, whereas males rarely entered the nest cavities. Female attentiveness then began to decline. Male attentiveness to the nest was sporadic until chicks were 10–12 days old, when all males began to enter their nests at least once each day. During late chick rearing, both male and female attentiveness were erratic and highly variable. Biologists may be able to use these results to identify nest problems and the need for management intervention when patterns of nest attentiveness deviate from the limits described in this study. *Received 26 Apr. 1994, accepted 15 Jan. 1995.*

Manipulation of reproductive behavior is often an important component of recovery programs for endangered birds. Behavioral manipulations have been used to increase productivity by inducing individuals to lay additional eggs through the removal of clutches (Cade 1977, Fyfe et al. 1977, Snyder and Hamber 1985), by artificially incubating eggs to increase hatchability (Cade 1977), and by hand-rearing or fostering into nests those chicks that otherwise would not have survived (Cade 1977, Meyburg 1977). "Hacking" and cross-fostering have been used to increase fledging rates in the wild (Fyfe et al. 1977, Meyburg 1977), to establish new populations (Drewien and Bizeau 1977, Kress 1977) and to establish new nest site or habitat preferences within a species (Cade 1977, Drewien and Bizeau 1977, Temple 1977).

The Puerto Rican Parrot (*Amazona vittata*) is critically endangered, with only 42 individuals remaining in the wild (1994 post-breeding survey, J. Meyers, pers. comm.). Monitoring and manipulation of reproductive behavior have been an important part of the U.S. Fish and Wildlife Service's Puerto Rican Parrot Recovery Program since 1973 (Snyder et al. 1987). Biologists have increased parrot productivity by inducing re-

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placement clutches, by fostering captive-produced young into wild nests, and by intervening when eggs or chicks are in jeopardy (Wiley 1981, 1985; Snyder et al. 1987; Lindsey 1992).

Because Puerto Rican Parrots nest in cavities and are sensitive to disturbance (Snyder et al. 1987, Wilson 1993), biologists responsible for monitoring parrots' nesting activities usually rely on behavioral cues from breeding pairs to determine if intervention is needed. Currently, evaluation of pair behavior depends largely on observers' personal experiences because few specific guidelines for identifying indicators of potential nest problems are available. Parrot managers, biologists, and nest observers (particularly new or seasonal personnel) need additional guidelines to maximize the effectiveness of nest monitoring and management.

The purpose of this study was to provide a detailed description of adult Puerto Rican Parrot nest attentiveness during successful nesting attempts.

STUDY AREA AND METHODS

During the study period, Puerto Rican Parrots nested in four distinct valleys within the Caribbean National Forest, an 11,300-ha section of the Luquillo Mountains in northeastern Puerto Rico (18°19'N, 65°45'W). All four valleys were within the Colorado Forest vegetation association described by Wadsworth (1951) and were dominated by palo colorado (*Cyrilla racemiflora*). Snyder et al. (1987) reported that three of the four areas included in our study were 510–625 m above sea level, received mean annual rainfall of 342.4–399.0 cm, and had an approximate temperature range of 16–29°C during 1974–1978. Although no data from the fourth valley in our study area were collected, we believe it possessed characteristics similar to those described above.

We (KAW and MHW) collected data and supervised data collection by 31 staff and volunteers in the nest guard program conducted by the U.S. Fish and Wildlife Service (Lindsey 1992). From February to August, 1987–1990, nests were monitored approximately 80–94% of all days in which a nest contained eggs or chicks (Lindsey 1992). Observers monitored nesting activity from blinds 10–30 m from each nest and recorded activities of breeding pairs. Individual parrots were identified primarily by size and pattern of the red blaze on each individual's forehead and secondarily by body shape and coloration. In 1989 and 1990, a microphone attached to a remote listening device was installed in each active nest; observers then monitored sounds in the nest cavity to confirm parrot movements.

In this paper, we examined only data from successful nesting attempts. We defined successful nesting attempts as those that involved no manipulation of eggs and that fledged at least one chick without the assistance of management intervention. We will examine adult behavior during failed nesting attempts in a separate publication.

We calculated the date that the first egg of each clutch was laid (day 0), based on inspections of each nest. If eggs were found during the first inspection, we assumed that one egg was laid every other day (Rodriguez-Vidal 1959, Low 1986, Snyder et al. 1987) and that no eggs were laid on the day of the inspection unless consecutive inspections indicated otherwise. If no inspection was performed during early stages of a nesting attempt, we backdated from estimated hatch dates, based on a 26-day incubation period (Snyder et al. 1987). Because Puerto Rican Parrots begin incubation between laying their first and second eggs in a 2- to 4-egg clutch (Snyder et al. 1987) and because nest inspections were infrequent during egg laying, the estimated error for calculation of egg laying date was ± 2 days. One nest that was relatively inaccessible had an estimated error for calculation of egg laying date of ± 5 days.

We divided the nesting cycle into four stages: egg laying (day −2 through day 6), incubation (day 7 through day 26), early chick rearing (day 27 through day 47), and late chick rearing (day 48 through fledging). We calculated mean, range, and standard error of the mean for five behavioral components for each day of the nesting cycle. Each data point (which represented the behavior of the male or female during one nesting attempt) included in these calculations was based on 15 h of observation per day (05:00–20:00, EST). Actual observation periods began at dawn (05:30–06:30) and ended at dark (18:00–19:30). We assumed that variations in actual daylight hours did not bias our results. Because breeding female Puerto Rican Parrots tend to roost in the nest cavity throughout the nesting cycle and because their mates tend to roost in the canopy near the nest tree (Snyder et al. 1987), we assumed that parrots did not enter or leave the nest in darkness. Data from days on which observers missed the parrots' movements (because of darkness or for other reasons) were not included in our calculations. Because of excluded data and because not all nests were observed on all days, the number of nesting attempts in our analysis (N) varied from day to day.

We examined five behavioral components. The first component, nest attendance, was measured as the percentage of a 15-h period that a parrot spent in its nest cavity. Our calculation of nest attendance included only periods when the parrots were in the cavity, not when they were perched on the nest lip or outside the cavity. Frequency of nest entries was the number of times a parrot entered its nest during a 15-h observation period. Mean attentive period was defined as the average time a parrot spent in its nest during each nest visit. Overnight attentive periods were not included in our calculations of mean attentive periods. Mean recess was the average time a parrot spent outside the nest each time it left the cavity. We calculated this component only for females. The fifth component, longest recess, was defined as the longest time a parrot spent away from its nest at any one time. We calculated this component only for females. Although these five behavioral components were interrelated, we described each component for the four stages of the nesting cycle to provide a more complete description of each parrot's behavior.

Nesting attempts by the same pair were not truly independent, but we treated each nesting attempt as a separate event because each new clutch offered the pair an opportunity to succeed or to fail in raising their young. Descriptive statistics were used to present the results of this study. More rigorous statistical tests were not applied to these data for two reasons. First, small sample size can lead to high probability of Type II error (Siegel 1956). Second, these data are not samples of a larger population but, to the best of our knowledge, the entire population of wild Puerto Rican Parrots that successfully reproduced during the study period.

Snyder et al. (1987) reported a similar data set that described behavior of Puerto Rican Parrots nesting in the Luquillo study area during 1973–1978. However, methods used by Snyder et al. (1987) to analyze raw data were sufficiently different from those used in our study that a direct comparison of these two data sets would have been inappropriate.

RESULTS

Eight of 15 nesting attempts observed during our data collection were classified as successful; one pair made three successful nesting attempts, one pair made two successful nesting attempts, and three pairs made one successful nesting attempt each. Six nesting attempts resulted in two fledged chicks each, and two attempts resulted in three fledged chicks each. Although no serious threats to reproductive success occurred during these nesting attempts, these nests did receive management attention. For example, all chicks were weighed periodically, and, in some cases, chicks were added, exchanged, or removed from nests (e.g., to increase genetic variability of the captive flock). However, in our judgment, these activities did not alter the likelihood of successful fledging of the remaining young.

Female parrots increased their nest attendance (Fig. 1), spent more time in their nests during each visit (Fig. 1), and took shorter recesses as egg laying progressed (Fig. 2). Three females exhibited no distinct trend in frequency of nest entries during egg laying, whereas one female, who entered her nest frequently during early egg laying, decreased her number of entries as she settled into incubation. Most males rarely entered their nests during egg laying (Fig. 3). One male, however, entered his nest frequently during early egg laying during two of his three nesting attempts. During these two nesting attempts, this male entered his nest less frequently and spent less total time on his nest as egg laying progressed.

During incubation, females maintained high levels of nest attendance (Fig. 1) and spent only brief periods away from their nests (Fig. 2). We found little variability in female nest attendance (Fig. 1), mean recesses (Fig. 2), or longest recesses (Fig. 2) within or among nesting attempts. No trend in frequency of nest entries was apparent (Fig. 1). After an incident of human disturbance (day 23), however, one female entered her nest more frequently and spent less time in her nest during each visit than did other females during this stage (Fig. 1). Males entered their nests infrequently during incubation and spent only brief periods in their nests when they did enter (Fig. 3).

During early chick rearing, females became less attentive to their nests (Fig. 1), whereas male attentiveness increased (Fig. 3). Females maintained high nest attendance during the first four days of early chick rearing (Fig. 1); thereafter, attendance declined, mean attentive periods became shorter (Fig. 1), and periods away from the nest increased (Fig. 2). Variability in female nest attendance (Fig. 1) and in duration of periods off the nest (Fig. 2) within and among nesting attempts also increased. Females tended to enter their nests more frequently during the first half of early chick rearing; their frequency of nest entries then stabilized (Fig. 1). High day-to-day variability within nesting attempts, however, obscured any trends in behavior of individual parrots. One female spent an unusually long time off her nest on day 41 following incidents of human disturbance on consecutive days; her mean recess increased, and her longest recess was more than twice as long as those of other females during this stage (Fig. 2). Males entered their nests sporadically during the first half of early chick rearing, but their nest attendance and frequency of entries

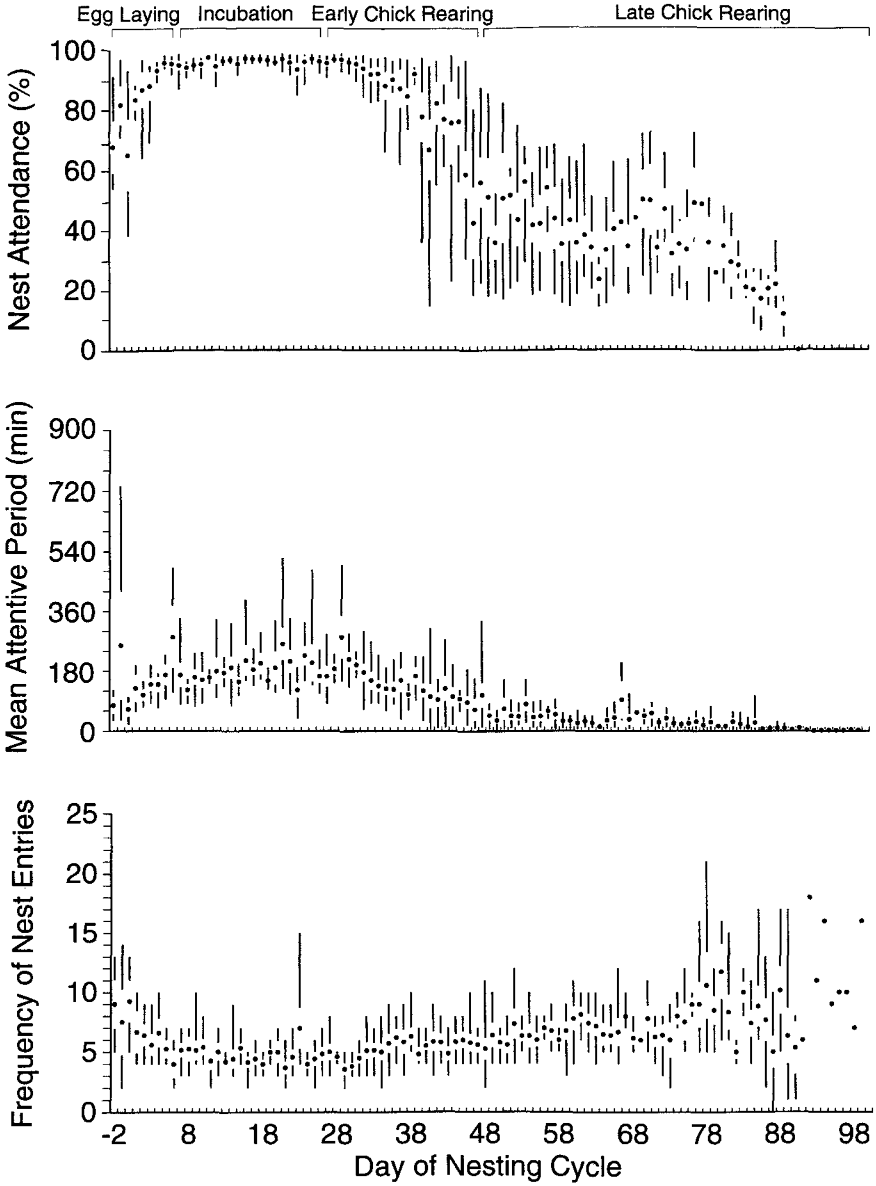

FIG. 1. Nest attendance (percentage of a 15-h period spent in the nest cavity), mean attentive periods (average period in nest during each visit), and frequency of nest entries (number of visits per day) by female Puerto Rican Parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Mean (black dots), standard error (gap in black bars), and range (black bars) are shown for all observed nests for each day of the nesting cycle. Sample size (N) varied daily from one to eight nesting attempts.

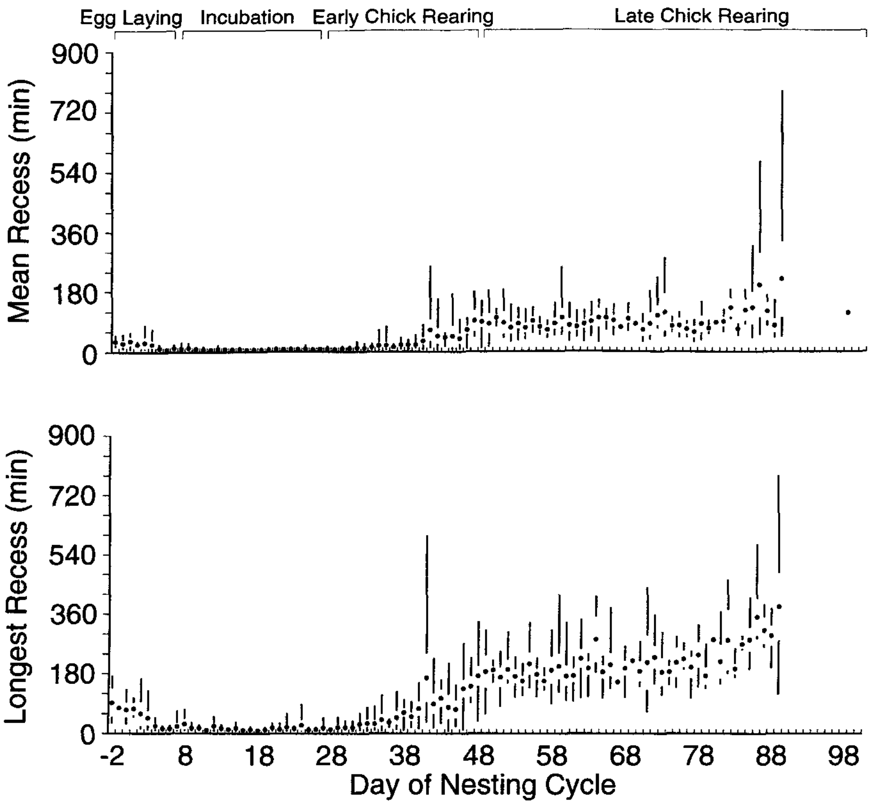

FIG. 2. Mean recesses (average period out of nest) and longest recesses (longest period out of nest) by female parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Other aspects of this figure are the same as those noted in Fig. 1.

generally increased as chick rearing progressed (Fig. 3). Except for one incident (one male on day 48), all males entered their nests at least once each day after their chicks were 10–12 days old (approximately day 38 of the nesting cycle) (Fig. 3).

During late chick rearing, female nest attendance varied erratically within and among nesting attempts (Fig. 1). At the end of the nesting cycle, however, females decreased their attendance (Fig. 1), spent less time in their nests during each visit (Fig. 1), and took longer recesses (Fig. 2). Variability in frequency of nest entries increased during the last several days of the nestling period as females entered their nests more frequently or fed their chicks from the nest lip as the chicks came to the top of the cavities (Fig. 1). Males entered their nests regularly and spent

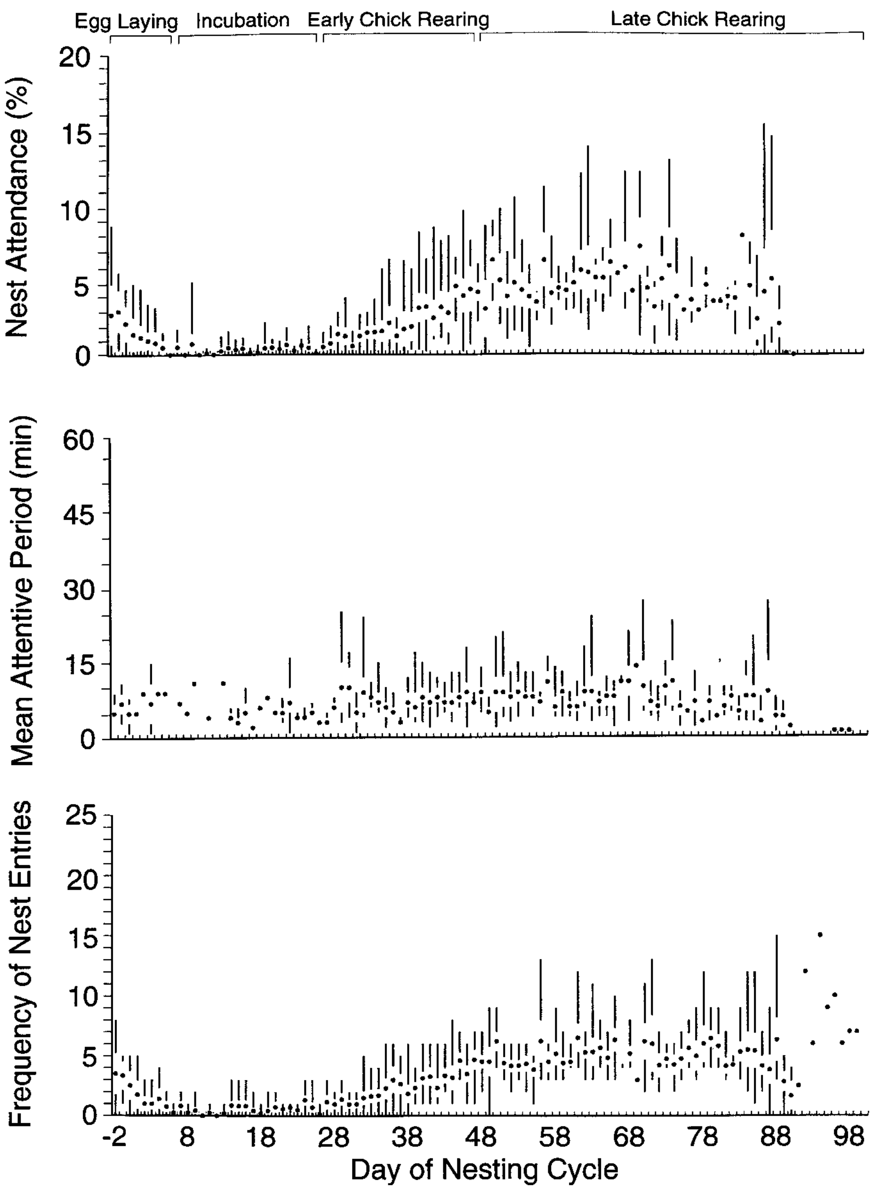

FIG. 3. Nest attendance (percentage of a 15-h period spent in the nest cavity), mean attentive period (average period in nest during each visit), and frequency of nest entries (number of visits per day) by male parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Note that the scale is different from that used in Fig. 1. Other aspects of this figure are the same as those noted in Fig. 1.

only brief periods of time in their nests throughout the late chick-rearing period; their behavior showed no distinct trends (Fig. 3). Like females, some males entered their nests more frequently and spent more time in their nests just prior to fledging of their young, whereas others fed their young from the nest lip (Fig. 3).

DISCUSSION

Puerto Rican Parrots that successfully raised their young exhibited distinct patterns of nesting behavior during incubation and early chick rearing. During incubation, females maintained high nest attendance and took only brief recesses from the nest, whereas males rarely entered nest cavities. Females spent less time in the nest as chick rearing progressed, whereas males entered their nests more frequently and increased their nest attendance. These distinct patterns of behavior reflect the importance of the incubation and early chick-rearing periods to successful reproduction, as eggs and young chicks are vulnerable to predation, temperature variation, and nutritional stress.

Although we observed little harassment of Puerto Rican Parrots by predators during our study, patterns of nest attentiveness exhibited by this species may be an adaptive response to predation pressure. Red-tailed Hawks (*Buteo jamaicensis*) have been reported to prey upon nestlings (Snyder et al. 1987) and fledglings (Lindsey et al. 1991) and have been observed harassing adults (Snyder et al. 1987). Unattended eggs and young chicks are vulnerable to predation or injury by Pearly-eyed Thrashers (*Margarops fuscatus*), introduced rats (*Rattus* spp.), and Puerto Rican boas (*Epicrates inornatus*) (Snyder et al. 1987). Infrequent nest entries may reduce the probability of revealing nest location to predators, whereas long attentive periods and high overall nest attendance allow almost constant defense of nest contents (Skutch 1957, 1962). Other behaviors of the Puerto Rican Parrot, such as the secretive movements of adults in the nest area and a tendency to allofeed close to the nest during incubation, also may reduce the conspicuousness of the nest and adults (Snyder et al. 1987).

Behavior of female parrots during early chick rearing reflects the changing thermoregulatory and nutritional needs of their young. Females maintain high nest attendance while chicks are dependent on almost constant brooding for survival; extended absences at this time can cause death of the young from exposure. Low (1986, 1987) noted that even if young do not succumb outright, chilling can leave them too weak to beg, increase their susceptibility to disease, and cause poor digestion and decreased growth rates. As the young develop thermoregulatory abilities, females spend more time away from their nests. Although Gnam (1991) found that size of Bahama Parrot (*Amazona leucocephala bahamensis*) broods did not affect the amount of time that females spent off the nest, Snyder et al. (1987) noted that female Puerto Rican Parrots with larger broods reached a plateau of time off the nest sooner than did females with smaller broods. Members of a brood tend to huddle together and, therefore, reduce the probability of chilling; however, larger broods also require more food. Females with larger broods may need to forage earlier in the nesting cycle for young to achieve optimal growth rates. There was too little variability in brood size in our study to make similar observations.

Behavior of males during early chick rearing appears to be related to nutritional needs of the young. Males almost invariably visited their nests daily (and presumably fed their young) after the chicks were approximately 10 days old; regular allofeeding by males may be essential for proper growth of the young at this time. During a nesting attempt reported by Snyder et al. (1987), chicks had notably slower rates of growth immediately following the loss of the adult male; although growth rates increased and the chicks later fledged, they remained underweight through the last recorded measurements at 34 and 37 days of age.

During late chick rearing, behavior within and among nesting attempts was highly variable. Nest attendance by females varied erratically, both within and among nesting attempts, and males showed no distinct patterns of behavior. We were unable to examine many potential causes of variability in this study because of small sample size and insufficient data; however, other authors have noted that variability in patterns of reproductive behavior of psittacines has been associated with previous reproductive experience (Noegel 1979; Thompson 1983; Low 1986, 1987; Stoodley and Stoodley 1990; Silva 1991), food supplies (Saunders 1977), weather (Saunders 1977, Gnam 1991), disturbance (Snyder et al. 1987, Wilson 1993), and individual differences (Low 1986, Stoodley and Stoodley 1990).

Aviculturists have noted that inexperienced *Amazona* often fail to provide adequate care for their young. For example, Low (1986, 1987) and Thompson (1983) noted that inadequate feeding of young by inexperienced *Amazona* is not uncommon. Although all pairs in our analysis fledged at least two chicks (which required adequate feeding and care of at least a partial brood), differences in previous experience among pairs may have accounted for some of the variability in behavior of adults among nesting attempts (e.g., frequency or duration of nest visits).

Saunders (1977) reported that White-tailed Black Cockatoos (*Calyptorhynchus baudinii latirostris*) that nested where food was patchily distributed spent less time in their nests and fed their chicks less frequently than did adults that nested in areas with more abundant food. Many of the most important food plants (particularly sierra palm, *Prestoea montana*) used by Puerto Rican Parrots are patchily distributed (Snyder et al. 1987); variability in behavior may reflect, in part, differences in the distances that pairs move in order to find food.

Female Bahama Parrots usually cease roosting in the nest by the fourth week post-hatching (Gnam 1991). However, Gnam (1991) noted that a female Bahama Parrot that had ceased roosting in the nest at night returned to brood during a period of heavy rainfall. In addition, Saunders (1977) noted that White-tailed Black Cockatoos spent less time foraging as temperature increased and therefore tended to feed their young less frequently on hot days. Although we did not measure precipitation or ambient temperature during our study, we know that three of the four valleys included in our study area received mean annual rainfall of 342.4–399.0 cm during 1974–1978 and are 510–625 m above sea level (Snyder et al. 1987). Differences in the location of each nest, as well as daily or annual variation in rainfall or the temperature fluctuations that often accompany rainfall, may have contributed to variability in nesting activities.

Disturbance from territorial intrusions by other parrots may cause defensive behavior by breeding pairs (Snyder et al. 1987). In extreme cases, excessive competition for nest sites has resulted in abandonment of active nests or injury to Puerto Rican Parrots (Snyder et al. 1987). In addition, human activities in nest areas affected the behavior of nesting females. During this study, females sometimes entered their nests more frequently and took longer recesses following incidents of human disturbance; Wilson (1993) provides a more detailed account of the effects of disturbance on the behavior of nesting adults.

Stoodley and Stoodley (1990) noted individual differences among female *Amazona* in frequency of allofeeding and in their ability to care for their young. Low (1986) noted that the age of the young when first fed by their male parent and the frequency of subsequent feedings varied among individual males. The relative contributions of inheritance and learning to such variation are unknown.

Although our sample size is small, our results indicated that a successful nesting attempt by Puerto Rican Parrots was characterized by well-defined patterns of attentiveness to the nest during incubation and early chick rearing. During incubation and the first several days of early chick rearing, females spent little time outside the nest and males rarely entered nest cavities. As chick rearing progressed, female nest attendance declined and males established a regular pattern of nest entries. Because these measures of attentiveness represented well-defined patterns of behavior, they may be particularly useful to parrot managers. If one assumes that variability of these measures defines the limits of normal behavior for each stage of the nesting cycle, deviations from the patterns described in this study may indicate nest problems that require management intervention.

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