BEHAVIOR OF PUERTO RICAN PARROTS DURING FAILED NESTING ATTEMPTS

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ABSTRACT.—We compared patterns of nesting behavior of four pairs of Puerto Rican Parrots (*Amazona vittata*) that experienced failed nesting attempts to behavior of four pairs of parrots that experienced no substantial nest problems and successfully fledged young without management intervention. Only changes in female parrots' behavior were clearly associated with nest failure. During incubation, decreases in nest attendance, increases in duration of recesses, and increases in frequency of nest entries by female parrots were associated with imminent abandonment of nests. During early chick rearing, similar behavior was associated with the loss of broods. Low nest attendance and long recesses by female parrots during incubation were also associated with successful hatching of eggs followed by death of young several days later. The behavior patterns and changes in Puerto Rican Parrot nesting behavior described in this paper may alert biologists to nest problems that might be mitigated by management intervention. *Received 7 May 1996, accepted 12 Feb. 1997.*

The Puerto Rican Parrot (Amazona vittata) is critically endangered, with a minimum of 38 individuals remaining in the wild (1996 pre-breeding survey, F. Nunez-Garcia, pers. comm.). Because of such small population size, monitoring and management of the wild flock are important components of the Puerto Rican Parrot Recovery Program and are vital to the parrot's continued recovery. To maximize fledging rates in the wild, for example, biologists routinely monitor and manipulate contents of active nests when eggs or young are believed to be in jeopardy. However, Puerto Rican Parrot nests in the wild are difficult to observe because they are located in deep tree cavities and because nesting adults are sensitive to disturbance. Therefore, biologists must often rely on behavioral cues from nesting adults to determine if intervention is needed. Currently, however, 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 in order 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 failed nesting attempts

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(those that were abandoned by the adults and those that resulted in the loss of the brood) in comparison to nest attentiveness by parrots that successfully fledged young and to identify behaviors associated with threats to reproductive success. Behavior of adult Puerto Rican Parrots during successful nesting attempts (those that involved no manipulation of eggs and fledged at least one chick without the assistance of management intervention) was described in an earlier publication (Wilson et al. 1995).

STUDY AREA AND METHODS

During the study period (1987–1990), Puerto Rican Parrots nested in four distinct valleys within the Caribbean National Forest, Puerto Rico ($18^{\circ}19'N$, $65^{\circ}45'W$). All four valleys are in the Colorado Forest vegetation association described by Wadsworth (1951). Snyder et al. (1987) reported that three of the four nesting areas included in our study are 510-625 m above sea level; during 1974–1978, these areas received mean annual rainfall of 342–399 cm and had an approximate temperature range of $16-29^{\circ}C$. Although no data describing 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 staff and volunteers in the Puerto Rican Parrot nest guard program (Lindsey 1992). Nests were monitored from dawn to dark from observation blinds during 80–94% of all days on which a nest contained eggs or chicks (Lindsey 1992). In 1989 and 1990, we also monitored vocalizations and movements within nest cavities by using a remote listening device attached to a microphone placed in each nest. More detailed methods are described in Wilson et al. (1995).

We calculated values for five behavioral components: nest attendance (for males and females), frequency of nest entries (for males and females), mean attentive period (for males and females), mean recess (females only), and longest recess (females only) for each day of the parrots' nesting cycle. Although these five behavioral components were partially interrelated, we described each component to provide a more complete description of each parrot's behavior. We divided the nesting cycle into four stages: egg laying (day -2 through 6), incubation (day 7 through 26), early chick rearing (day 27 through 47), and late chick rearing (day 48 through fledging). We then compared data from failed nesting attempts to data from successful nesting attempts described by Wilson et al. (1995).

We did not apply statistical tests to these data for two reasons. First, nesting attempts by the same pair were not truly independent. For purposes of descriptive analysis, however, 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. Second, small sample size (8 successful and 5 failed nesting attempts) can lead to high probability of Type II error (Siegel 1956). Instead, we defined the behavior of pairs that experienced failed nesting attempts as different from the behavior of pairs that successfully fledged young if (1) the duration or frequency of the behavior was at least 20% greater than the upper limit or at least 20% less than the lower limit of the range of values of the behavior by parrots that successfully fledged young or (2) the pattern or trend in values was different than the pattern or trend in values by parrots that successfully fledged young.

RESULTS

Four pairs (E1, E3, S1, S2) observed during this study failed to fledge young during a total of five nesting attempts (the S1 pair experienced two

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BRIEF SUMMARY OF EVENTS DURING FAILED NESTING ATTEMPTS BY PUERTO RICAN PARROTS, 1987–1990

Nest problem	Nesting attempt	Day	Event
Abandonment during incubation	E1	17	Pearly-eyed Thrasher entered nest. One egg damaged.
		25	Nest abandoned. Undamaged egg (pipping) re- moved to the Luquillo Aviary. Attempts to foster young into nest were unsuccessful.
Abandonment during incubation	E3	18	Puerto Rican boa approached nest. Eggs (all fertile) moved to the Luquillo Aviary and replaced with artificial eggs.
		26	Nest abandoned. Attempts to foster young into nest were unsuccessful.
Loss of brood	S1 _a	18	Intense vocal and physical interaction between breeding pair and conspecific intruders.
		45	Nest inspection. Two dead chicks partially consumed by insect larvae, one pipped egg with dead embryo. Attempts to foster young into nest were unsuccessful.
Loss of brood	S1 _b	41	Nest inspection. One dead chick, one live chick.
		66	Nest inspection. One dead chick. No attempts to foster young into nest.
Loss of brood (Loss of female)	S 2	32	Nest inspection. One dead chick, two eggs with dead embryos. Surrogate chicks suc- cessfully fostered into nest.
		71	Red-tailed Hawk lunged toward male.
		76	Female does not return to nest area. Presumed dead. Chicks removed from nest.

failed nesting attempts, $S1_a$ and $S1_b$, Table 1). Two pairs abandoned their nests during late incubation (E1 and E3). During three nesting attempts ($S1_a$, $S1_b$, and S2), two additional pairs lost their broods shortly after their chicks hatched.

We observed only minor differences during the egg-laying stage in the behavior of pairs that experienced failed nesting attempts compared to the behavior of pairs that successfully fledged young. During all stages of the nesting cycle, we observed only minor differences in the lengths of mean attentive periods of both males and females that experienced failed nesting attempts compared to lengths of mean attentive periods of those that successfully fledged young. We observed notable differences in the remaining behavioral components during some, but not all, other nesting stages as described below.

Female nest attendance.-During incubation, females exhibited differences in nest attendance during three of five failed nesting attempts observed (S1_a, E3, E1) compared to nest attendance by females that successfully fledged young (Fig. 1A, B, C). During the S1_a nesting attempt, the female tended to spend less time in her nest ($\bar{x} = 90.2\% \pm 0.8\%$ SE) throughout incubation than did females that successfully fledged young (range of daily mean: $\bar{x} = 93.2\% \pm 2.2\%$ SE to 97.4% $\pm 0.2\%$ SE) (Fig. 1A). This female $(S1_a)$ and the E3 female suddenly decreased their attendance during mid-incubation (days 13 and 18, respectively) (Fig. 1A, B). These decreases were associated with intense territorial defense against conspecific intruders (S1_a) and disturbance from a Puerto Rican boa (Epicrates inornatus) (E3) and resulting human activity. The S1_a female returned to her previous pattern of nest attendance on day 14 (Fig. 1A). Although the E3 female generally became more attentive following the boa's visit, she exhibited a second drop in attendance just prior to abandoning her nest on day 26 (Fig. 1B). During the third nesting attempt, the E1 female exhibited a pattern of erratically decreasing nest attendance in association with numerous incidents of disturbance by predators (i.e., Pearly-eyed Thrashers, [Margarops fuscatus]) and resulting human activities before finally abandoning her nest (Fig. 1C).

During early chick rearing, females exhibited changes in patterns of nest attendance during two of three nesting attempts observed during this stage (S1_a and S2, Fig. 1A, D). During the S1_a nesting attempt, the female's pattern of attendance was comparable to that of females that successfully fledged young until day 44, when her attendance suddenly decreased (Fig. 1A). We confirmed the deaths of her young the following day. During the S2 nesting attempt, the female's attentiveness unexpectedly decreased two days before we confirmed death of her young (Fig. 1D). Following successful fostering of surrogate Hispaniolan Parrot (*Amazona ventralis*) young into the S2 nest, however, the female resumed a pattern of attendance comparable to that of successful females (Fig. 1D).

During late chick rearing, the S1_b female maintained relatively high nest attendance ($\bar{x} = 73.6\% \pm 2.2\%$ SE) compared to nest attendance of females that successfully fledged young (range of daily $\bar{x} = 23.4\% \pm 4.9\%$ SE to 55.9% $\pm 8.3\%$ SE) (Fig. 1E). The S2 female maintained nest attendance comparable to that of females that successfully fledged young until her disappearance on day 76.

Frequency of female nest entries.—During early chick rearing, the $S1_a$ female entered her nest more frequently than did females that fledged



FIG. 1. Nest attendance (percentage of a 15-h period spent in nest cavity) by female Puerto Rican Parrots during failed nesting attempts (circles) shown with range (bars) of nest attendance by female parrots that fledged young, 1987–1990. Arrows indicate day that nest was abandoned or nest failure was discovered. Triangles represent behavior of parrots with surrogate young.



FIG. 2. Frequency of nest entries (number of visits per day) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

young (Fig. 2). The frequency of nest entries increased on day 43 and exceeded the expected range of frequency of nest entries on day 44, one day before we confirmed nest failure (Fig. 2). Her frequency of nest entries became erratic during attempts to foster surrogate young into the nest. All other females entered their nests at a rate comparable to that by females that successfully fledged young.

Female mean recess.-During incubation, females exhibited differences in mean recesses during four nesting attempts (S1, E3, E1, and S2; Fig. 3A, B, C, D, respectively) compared to mean recesses by females that successfully fledged young. During the S1, nesting attempt, the female frequently took long mean recesses ($\bar{x} = 17.6 \text{ min} \pm 1.9 \text{ min} \text{ SE}$) throughout incubation compared to mean recesses of females that successfully fledged young (range of daily $\bar{x} = 5.8 \text{ min } \pm 0.7 \text{ min SE}$ to 12.8 min \pm 5.3 min SE). This female and one other female, E3, unexpectedly increased the length of their mean recesses during mid-incubation (days 11-13 and 18, respectively, Fig. 3A, B). The two females that abandoned their nesting attempts (E3 and E1) began to take longer mean recesses one to two days prior to abandonment (Fig. 3B, C). One female (S2) suddenly increased the average time she spent off her nest one day before we confirmed the loss of her young (Fig. 3D). Following successful fostering of surrogate young, however, this female's mean recesses were comparable to those of females that fledged young (Fig. 3D).

Longest female recess.—During incubation, females exhibited differences in longest recesses during three nesting attempts (S1_a, E3, and E1) compared to longest recesses by females that fledged young (Fig. 4A, B, C). During two nesting attempts (S1_a and E3), females suddenly increased their longest recesses during mid-incubation (days 13 and 18 respectively, Fig. 4A, B). During nesting attempt E1, the female's pattern of longest recesses became erratic during the latter half of the incubation period (Fig.



FIG. 3. Mean recesses (average period out of nest) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

4C). Both the E3 and E1 females tended to spend more time away from their nests during their longest recesses one to two days prior to abandoning their nests (Fig. 4B, C).

During early chick rearing, females unexpectedly increased their longest recesses during two nesting attempts (S1_a and S2, Fig. 4A, D). One female's (S1_a) longest recesses increased at a rate comparable to that of successful females until we confirmed the loss of her young (Fig. 4A). Her longest recesses then became erratic and were likely affected by our



FIG. 4. Longest recesses (longest period out of nest) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

attempts to foster surrogate young into her nest (Fig. 4A). During the S2 nesting attempt, the female showed an unexpected sharp increase in her longest recesses on day 30, two days before we confirmed loss of her young (Fig. 4D). Following successful fostering of surrogate young into her nest, however, this female resumed a pattern of longest recesses comparable to that of females that successfully fledged young (Fig. 4D).

During late chick rearing, the S1_b female took only short recesses from her nest ($\bar{x} = 103.1 \text{ min } \pm 13.2 \text{ min SE}$). Females that successfully fledged young frequently left their nests for much longer periods (range of daily $\bar{x} = 144.3 \text{ min } \pm 12.1 \text{ min SE}$ to 281.7 min $\pm 68.5 \text{ min SE}$) (Fig. 4E).

Male nest attendance and frequency of male nest entries.—During incubation, the E1 male often entered his nest more frequently and spent more time in his nest than did males that successfully fledged young. He entered his nest most frequently and maintained particularly high nest attendance during the four days before he abandoned his nest (Figs. 5A, 6A).

During early chick rearing, the $S1_a$ male failed to establish a regular pattern of at least one nest entry per day (Fig. 6B). Except for one incident (one male on one day, day 48), all successful males tended to enter their nests regularly after day 38 and most males established a regular pattern of daily visits before this time (Wilson et al. 1995). In addition, the $S1_a$ male, who generally entered his nest less than three times per day during early chick rearing, showed a sudden increase in nest entries on day 44, one day before we confirmed the deaths of his young (Fig. 6B).

During late chick rearing, one male's $(S1_b)$ nest attendance and frequency of nest entries were notably different from the behavior of males that successfully fledged young (Figs. 5C, 6C). This male's nest attendance and frequency of nest entries had been comparable to those of successful males during early chick rearing; however, on days 48, 50, and 51, he did not enter his nest (Fig. 5C), whereas successful males entered their nests at least once per day during this same period. His nest attendance ($\bar{x} = 1.7\% \pm 0.6\%$ SE) and frequency of nest entries tended to be low during the remainder of observation compared to nest attendance (range of daily $\bar{x} = 3.4\% \pm 0.6\%$ SE to $6.2\% \pm 1.7\%$ SE) and frequency of nest entries by males that successfully fledged young (Figs. 5C, 6C).

DISCUSSION

The most common behavioral aberrations among parrots that abandoned their nests during incubation were low nest attendance and long absences from the nest by adult females. The two females that abandoned nests during incubation exhibited decreased nest attendance, increasing



FIG. 5. Nest attendance (percentage of a 15-h period spent in nest cavity) by male Puerto Rican Parrots during failed nesting attempts. Note scale is different than scale used in Fig. 1, otherwise all symbols are the same.

mean recesses, and increasing longest recesses one to two days prior to abandonment. However, only one of two males that abandoned their nests exhibited differences in behavior prior to abandonment. The male began to spend more time in his nest and to enter his nest more frequently four days prior to abandoning his nesting attempt.

Females that lost their broods exhibited behavior similar to those that abandoned their nesting attempts during incubation. Females that lost their broods exhibited unexpected declines in nest attendance and either took longer recesses or entered their nests more frequently one to two days prior to our discovery of the loss of their young. Therefore, unexpected declines in female nest attendance accompanied by increases in the length of female recesses or in frequency of female nest entries may be the most reliable indicators of imminent nest abandonment resulting from a variety of causes. We also noted that parrots often give "whining"



FIG. 6. Frequency of nest entries (number of visits per day) by male Puerto Rican Parrots during failed nesting attempts. All symbols are as given in Fig. 1.

or "wailing" vocalizations during "high anxiety" situations such as intense territorial defense, nest abandonment, and loss of a brood, but we did not have adequate data to determine if such vocalizations could be used as indicators of threats to reproductive success.

Although differences in the behavior of female parrots were clearly associated with nest failure during this study, whether such behavioral changes contributed to or caused the death of embryos and young is unknown. Well-developed embryos and older chicks can withstand cooling (Low 1987, Snyder et al. 1987, Jordan 1989); however, incidents of embryo chilling and low incubation temperatures in captivity can lead to embryonic mortality, hatching failure, or successful hatching of small, weak chicks and/or death of chicks at a young age (Low 1987, Van Der Heyden 1987, Jordan 1989, Kuehler and Good 1990, Stoodley and Stoodley 1990). Little is known about the effects of temperature variation on parrot embryos and young in wild nests. Embryos and/or young from three nesting attempts observed during this study (E1, E3, and S1_a) may have been exposed to chilling by low nest attendance and/or long absences from the nest by females during incubation. However, these embryos also experienced other conditions that may have affected their survival. The E3 and E1 embryos, which were removed from the nests and completed incubation/hatching in captivity, may have been stressed or damaged by jarring experienced during transport from field to aviary (Kuehler and Good 1990, Stoodley and Stoodley 1990). The S1_a brood had been mostly consumed by insect larvae by the time we inspected the nest; whether infestation occurred prior to (Snyder et al. 1987) or following death of the young is unknown.

Similarly, the pattern of chronically low frequency of nest entries exhibited by the $S1_a$ male during early chick rearing may have affected the survival of his young directly, may have resulted from the chicks' behavior, or may have been unrelated to failure of his nesting attempt. Because other males tended to enter their nests regularly to feed their young (Wilson et al. 1995; KAW and MHW, pers. obs.), a chronically low frequency of nest entries by males may indicate inadequate feeding of the young. If we assume that males are stimulated to enter their nests by vocalizations of the young, infrequent entries may also result from ailing chicks that beg less frequently or less vigorously. We do not have data to support or refute any of these explanations.

We believe that behaviors that appeared one to two days prior to our discovery of the loss of a brood (as opposed to those that occurred earlier in the nesting cycle) during this study were the result of the absence of stimuli ordinarily provided by healthy young rather than the proximate cause of the loss. Both pairs that lost a brood during early chick rearing $(S1_a \text{ and } S2)$ had successfully raised several previous broods, and we observed no other circumstances that might have stimulated declining interest in a nest (e.g., disturbance, Wilson 1993, Wilson et al. 1995). Also, we have no other records of declining attentiveness by Puerto Rican Parrots without the presence of potential causes of such behavior.

Although behavior of the $S1_b$ pair was notably different throughout late chick rearing than that of pairs that successfully fledged young, we believe their behavior was unrelated to the loss of their brood. The oldest chick, which appeared to have beak and neck abnormalities and poor growth, died at approximately 15 days of age (i.e., during early chick rearing) from unknown causes. The remaining chick died on day 66 after exhibiting symptoms of the "growth syndrome" that afflicted one chick of each brood from this nest during all four years of the study period. Typical symptoms of the syndrome include suspended weight gain at 180 g, poor feather growth, susceptibility to infection and ultimately death in spite of intensive veterinary care. Given the nature and incidence of the illness, the syndrome may be of genetic origin. Behavior of the pair may have been related to scarcity of Sierra palm (*Prestoea montana*) fruit, the parrots' primary food source during the breeding season (Snyder et al. 1987), caused by almost complete defoliation of vegetation during Hurricane Hugo in September of 1989. However, another pair nesting in a different valley successfully raised three young later that same season.

A likely explanation for the high attendance by the $S1_{h}$ female and infrequent nest visits by the S1_b male during late chick rearing is small brood size (1 young). Snyder et al. (1987) found that females with a single chick tended to maintain high nest attendance later in the nesting cycle than did females with larger broods. During our study, we observed such consistently high female nest attendance during late chick rearing during only one other nesting attempt (a successful attempt, Wilson et al. 1995) which also contained only one chick during the first part of the late chick rearing stage. Similarly, the S1_b male exhibited behavior like that of the male of the successful nesting attempt noted above. On days 48, 50, and 51, the $S1_{h}$ male did not enter his nest, whereas he had previously entered his nest one to six times per day. The successful male also suddenly failed to enter his nest on day 48. Although other factors might affect a male parrot's attentiveness (Wilson 1993, Wilson et al. 1995), we observed no change in levels of conspecific activity, human activity, or vocalizations by the chick prior to or during the $S1_{h}$ male's decline in nest attendance.

Although the implications of these results are limited by small sample size, this study provides an initial detailed description of Puerto Rican Parrot reproductive behavior during failed nesting attempts. Observers should now be able to identify behavior indicative of nest problems and take appropriate management action. Upon recognition of these behaviors, biologists can remove eggs or chicks from nests threatened by abandonment and replace them with artificial eggs or surrogate young until the behavior of the pair returns to acceptable levels. Ill or injured young can be removed from nests for treatment and replaced with young of a surrogate species or with other Puerto Rican Parrot young. Even if biologists are unable to prevent deaths of embryos and young, maintenance of nesting activity by fostering may prevent pairs from adopting different and perhaps less suitable nest sites the following season (Wiley 1983).

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