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Effects of laying date, clutch size, and communal nest size on the reproductive success of Monk Parakeets.—Monk Parakeets (*Myiopsitta monachus*) build conspicuous, enclosed stick nests, which are often large and which have several isolated chambers (Forshaw 1978, Martella and Bucher 1993). These chambers are occupied throughout the year by breeding pairs and non-breeding individuals (Martín 1989, Martella and Bucher 1993). The Monk Parakeet is iteroparous, monogamous, and breeds in the spring and summer (October to February) (Navarro et al. 1992). Although all members of a compound nest participate in the building, maintenance, and vigilance of the nest, only the breeding pair cares for the nestlings (Martella 1985, Martella and Bucher 1993). Few cases of allofeeding by members of different nests have been observed, which could function for the development of a communal breeding system (Martella 1985, Bucher et al. 1991).

Monk Parakeets have a variable clutch size (Navarro et al. 1992), the adaptive nature of which has been the subject of extensive discussion (e.g., Lack 1954, Perrins and Jones 1974). However, except for the research of Beissinger and Waltman (1991) on the Green-rumped Parrotlet (*Forpus passerinus*), this topic has been little studied in parrots.

In this paper we examine how laying date, clutch size, and the size of communal nest affect the reproductive success of Monk Parakeets.

Study areas and methods.—This study was carried out in 1982 near the town of Arroyito (31°25′S, 62°59′W) and from 1983 to 1988 close to the city of Jesús María (31°05′S, 64°11′W), in Córdoba Province, Argentina. Overall, we recorded 205 breeding attempts. Nest chambers were checked at seven to 12-day intervals from October to early March. This interval was selected to avoid a reduction of the breeding success due to observers disturbance (Navarro et al. 1992). In Arroyito, sampled nests were all grouped in *Eucalyptus* trees planted at both sides of the 1000-m long entrance to the ranch. In J. María, all nests were in the 610-ha study area in native trees. We could not sample very large nests (with more than ten individuals) because they were on inaccessible structures on powerline towers, windmills and tall trees. However, large nests comprised only 2% of the nests in both areas (Bucher et al. 1991).

Eggs found in each nest chamber were marked individually with indelible ink. Nestlings were identified by clipping different toenails and later were banded with numbered aluminum rings. The fate of each egg was recorded as either lost before hatching, failed to hatch, or hatched. Eggs that might have hatched but whose chicks disappeared before the following visit were assumed not to have hatched. Nestlings that disappeared from the nest before reaching fledging age (35 days; Navarro and Bucher 1990) were recorded as deaths. In doubtful cases, the survival was checked through capture-release procedures carried out three times a year during all the study (Navarro 1989; Martín and Bucher 1993). Initiation dates for clutches were determined by back-dating each clutch based on a 2.1-day interval between successive eggs, a 24-day incubation period (Navarro 1989), and the calculated age of nestlings (Navarro and Bucher 1990). Twenty-two clutches in which we could not estimate the onset of laying were discarded. To compare dates among years, we used the distance in days of a given date from the median date of first clutch for the population in that year, assigning negative values to those dates earlier than the median. First clutches refer to the first group of eggs laid in a given nest chamber in that season, replacement clutches are those started after failure of the first clutch, and second clutches are those laid after a successful first brood.

Results.—The earliest clutch was laid on 1 October 1983 and the latest on 29 October 1985. At both areas, 90% of first clutches within the population were laid within a nine week period (see also Navarro et al. 1992; Navarro and Bucher 1992). Clutch sizes ranged

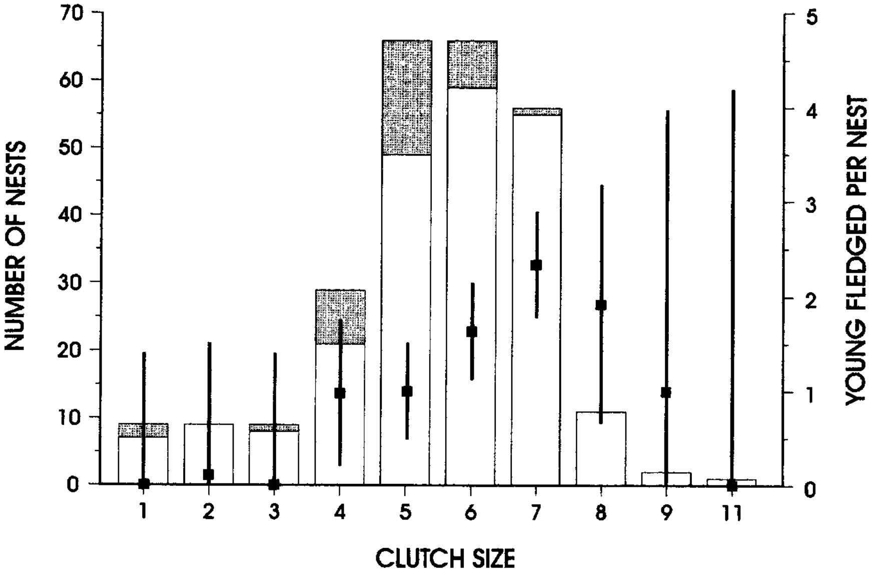

FIG. 1. Clutch size frequency (bars) and fledging success (squares) in Monk Parakeets. Open bars represent first clutches; shaded bars are replacement and second clutches. Vertical lines indicate 95% Tukey's HSD intervals above and below mean values.

from one to 11 eggs (mode = 6 eggs in first clutches); whereas replacement and second clutches ranged from one to seven eggs (mode = 5 eggs) (Fig. 1). First-clutches were significantly larger than second and replacement clutches (Mann-Whitney test; $Z = 3.27$; $P = 0.001$).

Clutch size decreased with the date of laying. As the breeding season advanced, first clutches were smaller (Spearman Rank Correlation; $r_s = -0.290$, N = 200, $P < 0.001$).

Hatching success was significantly correlated to laying date and clutch size. Hatching success decreased throughout the nesting season when a partial correlation was used to hold clutch size constant (Partial Correlation coefficient; $R_p = -0.225$, N = 200, $P < 0.01$), and, in turn, increased with the clutch size when laying date was held constant ($R_p = 0.332$, N = 200, $P < 0.01$).

Fledging success was not correlated with either laying date ($R_p = -0.050$, N = 200, $P > 0.05$) or clutch size ($R_p = 0.123$, N = 200, $P > 0.05$) when clutch size and relative laying date were held constant, respectively.

As a result of both the greater number of eggs and the higher hatching success of larger clutches, the number of young fledging per pair increased with clutch size. The most productive clutches were those of seven eggs, but they did not differ significantly from clutches of six or ≥ eight eggs (Fig. 1). Virtually none of the clutches of one to three eggs successfully fledged young (Fig. 1). The low frequency of these small clutches led us to think that they could be the result of undetected layings and subsequent predation (between visits), or due to the desertion or death of at least one member of the pairbond. Furthermore, their low productivity is likely to be a consequence of any of these factors.

Laying date of first clutches did not affect wether females laid a replacement or second clutch. Early and late breeders did not differ in the frequency of starting replacement or second clutches ($\chi^2 = 0.155$, df = 1, $P = 0.7$). Nevertheless, the date of the onset of laying had a significant effect on the chances of producing at least one young from the first clutch. Early breeding pairs (those that began their first clutch before the respective median date of each year) produced at least one young in 55% of the first clutches started compared to only 39% for late breeders ($\chi^2 = 4.79$, df = 1, $P = 0.029$).

Laying date of first clutches was significantly negatively correlated with the number of parakeets inhabiting compound nests ($r_s = -0.256$, N = 184, $P < 0.001$). First clutches were laid earlier in larger nests. Hatching success and fledging success of first clutches had positive but non-significant relationships with the number of individuals occupying the compound nest, when the date of onset of laying was held constant by partial correlation (R_p = 0.140 and R_p = 0.083, N = 184; respectively).

The productivity of a nest chamber depended on the date of laying but not on the number of individuals inhabiting the compound nest to which it belongs. The total number of young fledged from a nest chamber throughout the season (considering all clutches that had been laid) was significantly correlated with the laying date of first clutch when the number of individuals in the compound nest was held constant ($R_p = -0.262$, N = 184, $P < 0.01$). On the other hand, when date was held constant, the number of young produced was not correlated with the number of individuals inhabiting the nest (R_p = 0.075, N = 184).

Overall, the total number of young fledged from breeding chambers in compound nests that were occupied by more than four birds (median value) was higher (but not significantly) than fledging success of smaller nests ($Z = 0.693$; N = 43 and 162, respectively; $P = 0.488$). Also, the proportion of successful breeding pairs (first clutches only) in nests inhabited by more than four birds (55.8%) was higher (but not significantly) than that of smaller nests (42.6%) ($\chi^2 = 2.397$; df = 1; $P = 0.122$). This difference was even lower when first and non-first clutches were considered together.

Discussion.—Our results show that the date of laying was the most important correlate of reproductive success in Monk Parakeets. Laying date correlates both with the clutch size and hatching success, so on average early clutches are larger and produce more nestlings and, consequently, more fledglings than late clutches (because the fledging success is independent of date and clutch size). This result coincides with the observations of Beissinger and Waltman (1991) in Green-rumped Parrotlet, in which the number of young increased with clutch size. In addition, in the Monk Parakeet early clutches are more likely to produce at least one juvenile than late clutches.

There is a slight trend by breeding pairs inhabiting large nests to start egg laying earlier in the season. In larger nests, interactions among individuals such as social stimulation, self-maintenance behavior (e.g., foraging) and nest construction and maintenance, are facilitated (e.g., all members of a compound nest participate in bringing material to the nest and in building and maintenance activities) (Bucher et al. 1991, Martella and Bucher 1993). These interactions seem to play an important role in the Monk Parakeet breeding system (Martella 1985, Bucher et al. 1991), and could promote earlier laying attempts.

Despite the above mentioned trend, individuals inhabiting larger nests do not have, on average, a significantly higher productivity nor chances of being successful with their first clutch compared to individuals at smaller nests. Larger nests are frequently occupied simultaneously (in different chambers) by adults with breeding experience and inexperienced breeders (two-year-olds; Martella 1985, Martín and Bucher 1993). Taking into account that either experienced or novice breeders are physiologically capable of breeding, and that egg laying could be not as costly to females as rearing the young, as proposed by Waltman and Beissinger (1992) in Green-rumped Parrotlet, one can expect that all pairs should begin a clutch. However, unskilled breeders could not always be "ready" (see below) for facing the effort of taking care of a large brood. Therefore, the lower success of inexperienced breeders could be contributing to reduce the average productivity of large communal nests.

Given that the Monk Parakeet is a long lived species (about 5 years on average and 12 years maximum; Martín 1989), the reduction of its reproductive output could be explained by the "restraint" hypothesis, the "constraint" hypothesis, or a combination of both (Curio 1983). If additional breeding effort required to rear a large brood under unfavorable conditions could reduce the individual's probability of subsequent survival, young Monk Parakeets should refrain from investing maximally in actual reproduction and should increase their breeding effort as they become older to maximize lifetime reproductive success. Besides, the less successful breeding attempts may allow Monk Parakeets to gain experience and, therefore, to improve their breeding performance in following breeding seasons.

Lack's (1954) suggested that the most common clutch size should be the most productive. However, the Monk Parakeet's modal clutch size (six eggs) was not more productive than larger clutch sizes. This argues against Lack's prediction, but agrees with other studies in parrots (Smith and Saunders 1986, Beissinger and Waltman 1991) and other bird species in which deviations from Lack's principle have been ascribed either to differences in female age, experience and condition, or to territory quality (e.g., Klomp 1970, Winkler and Walters 1983). Under the assumption that reproductive restraint or constraint hypotheses are operating, one could expect that the frequency distribution of clutch sizes of Monk Parakeets would not fit to Lack's (1954) predictions.

All above mentioned issues are closely related and, as consequence, this study is not conclusive about the forces driving the reproductive success in the Monk Parakeet. Although under field conditions it could be difficult to tease apart their effect, further research focused on these topics is required.

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LITERATURE CITED

BEISSINGER, S. R. AND J. R. WALTMAN. 1991. Extraordinary clutch size and hatching asynchrony of a neotropical parrot. Auk 108:863–871.

BUCHER, E. H., L. F. MARTIN, M. B. MARTELLA, AND J. L. NAVARRO. 1991. Social behaviour and population dynamics of the Monk Parakeet. Acta XX Congressus Internationalis Ornithologici:681–689.

CURIO, E. 1983. Why do young birds reproduce less well? Ibis 125:400–403.

FORSHAW, J. 1978. Parrots of the world. Landsdowne Editions. Melbourne, Australia.

KLOMP, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1–124.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford, England.

MARTELLA, M. B. 1985. Observaciones sobre el comportamiento de la cotorra *Myiopsitta monachus* con especial énfasis en la comunicación sonora. Ph.D. diss. Univ. Nac. de Córdoba, Córdoba, Argentina.

——— AND E. H. BUCHER. 1993. Estructura del nido y comportamiento de nidificación de la cotorra *Myiopsitta monachus.* Boletín de la Soc. Zool. del Uruguay 8:211–217.

MARTIN, L. F. 1989. Características del sistema social cooperativo de la cotorra *Myiopsitta monachus.* Ph.D. diss. Univ. Nac. de Córdoba, Argentina.

——— AND E. H. BUCHER. 1993. Natal dispersal and first breeding age in Monk Parakeets. Auk 110:930–933.

NAVARRO, J. L. 1989. Dinámica poblacional de la cotorra (*Myiopsitta monachus*). Ph.D. diss. Univ. Nac. de Córdoba, Argentina.

——— AND E. H. BUCHER. 1990. Growth of Monk Parakeets. Wilson Bull. 102:520–525.

——— AND ———. 1992. Annual variation in the timing of breeding of the Monk Parakeet in relation to climatic factors. Wilson Bull. 104:545–549.

———, M. B. MARTELLA, AND E. H. BUCHER. 1992. Breeding season and productivity of Monk Parakeets in Córdoba, Argentina. Wilson Bull. 104:413–424.

PERRINS, C. M. AND P. J. JONES. 1974. The inheritance of clutch size in the Great Tit. Condor 76:225–229.

SMITH, G. T. AND D. A. SAUNDERS. 1986. Clutch size and productivity in three sympatric species of cockatoo (Psittaciformes) in the South-West of Western Australia. Aust. Wildl. Res. 13:275–285.

WALTMAN, J. R. AND S. R. BEISSINGER. 1992. Breeding behavior of the Green-rumped Parrotlet. Wilson Bull. 104:65–84.

WINKLER, D. W. AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Pp. 33–68 *in* Current Ornithology Vol. 1 (R. F. Johnston, ed.). Plenum Press, New York, New York.

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The influence of Yellow-bellied Sapsuckers on local insect community structure.— Natural communities consist of irregular patchworks of organisms whose relative abundances both reflect and influence environmental heterogeneity (e.g., Diamond and Case 1986, Cornell and Lawton 1992). Within a given habitat, any species that augments environmental patchiness is likely to influence the abundances of sympatric species. For instance, through their unusual foraging strategy, Yellow-bellied Sapsuckers (*Sphyrapicus varius*) create rich resource patches in the form of sapwells, and may thereby affect population densities and spatial distributions of many co-occurring species.

The Yellow-bellied Sapsucker feeds primarily on phloem and sap obtained through the excavation of sapwells. A sapwell consists of horizontal rows of shallow holes drilled into bark, into which sap flows (Tate 1973). Sapsuckers drill newer rows directly above older wells, producing a two dimensional array of shallow holes. While the volume and quality of sap flow depend on both the tree species and the daily rates of transpiration and photosynthesis (Foster and Tate 1966), flow can often be considerable and sap often contains 20–30% sucrose (Tate 1973). Insects comprising seven orders and 20 families have been found associated with sapwells (Foster and Tate 1966). Preferential orientation of insects toward rich resource patches may be manifest as increased abundance and/or diversity of nectivorous insect communities in close proximity to sapwells. Therefore, by serving as a focal point for insect aggregation, sapwells may influence the local community structure (i.e., absolute and relative abundances) of the nectivorous insect guild. The purpose of this study was to determine (1) whether sapsucker foraging influences local insect diversity and species