HABITAT SELECTION BY THE MONK PARAKEET DURING COLONIZATION OF A NEW AREA IN SPAIN[1]

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Abstract. The Monk Parakeet (*Myiopsitta monachus*) is a habitat generalist parrot from South America that has been introduced to and has expanded its range in Europe and North America. The aim of this study was to examine habitat selection in Monk Parakeets during the colonization of Barcelona, Spain, from 1992 to 1994. The Monk Parakeet showed a great selectivity in habitat choice, contrasting with the generalist behavior of the species in South America. The species inhabited urban parks with edible plants and palms (*Phoenix* spp.). Individuals showed a great specificity and preference for nesting in palms and palms appeared to be the main factor influencing the distribution and abundance of parakeets. Individuals showed a consistent preference for nesting in the tallest palms, probably as a way to reduce predation and human disturbance, although other characteristics also could affect the nest location. Implications of these findings for the biology and management of the species are discussed.

Key words: Monk Parakeet, Myiopsitta monachus, *invasive species, habitat selection, nest-site selection.*

INTRODUCTION

The study of biological invasions is an important area of current ecology because it is essential to understanding relevant ecological processes and to predict the ecological and economic impact of exotic species (Drake et al. 1989, Temple 1992, Lodge 1993). Nevertheless, for most exotic birds little more than their presence has been recorded (Temple 1992). One approach to understanding the interaction among exotic birds and native communities involves the study of habitat selection. The aim of this paper is to analyze the habitat selection of an introduced bird, the Monk Parakeet (*Myiopsitta monachus*), during colonization of a new area.

The Monk Parakeet is a medium-size parrot native to South America (Forshaw 1989), where it is an agricultural pest (Bucher et al. 1990). Parakeets are trapped massively throughout their native range and exported to other countries for the pet trade (Bucher et al. 1990), which has permitted the establishment of feral populations where individuals escaped or were released. Today the species occurs in Belgium (De Schaetzen and Jacob 1985), Italy (Spanò and Truffi 1986), Spain (Clavell et al. 1991),

and the United States (Hyman and Pruett-Jones 1995, van Bael and Pruett-Jones, in press).

Considerable information is available about Monk Parakeets, based upon studies in their native range (Bucher and Martin 1987, Forshaw 1989, Bucher et al. 1990, Martella and Bucher 1990). They are nonterritorial, highly social parrots with a very complex communication system. In its native range, this parakeet is primarily a sedentary, lowland bird, that lives in a great variety of habitats such as open forests, trees along watercourses, savanna woodlands, dry *Acacia* scrubland, palm groves, farmlands, orchards, and urban parks. Individuals forage both in trees and on the ground and their diet consists of seeds, fruits, berries, nuts, leaf buds, and blossoms of a great variety of plants and, in some cases, insect larvae. The species is unique among parrots in building its own nest of sticks, which are often integrated in a compound nest containing several isolated chambers. Nests are generally built in trees or electric poles, and parakeets continue to roost within their nests throughout the whole year.

In the mid-1970s, the Monk Parakeet (subspecies *M. m. monachus*) became established in the city of Barcelona, Spain (Batllori and Nos 1985), and since then the species has dramatically increased its population and expanded its range (Clavell et al. 1991). In this paper we examine the habitat selection by Monk Parakeets

while colonizing the city from 1992 to 1994. Our objectives were to (1) assess the influence of food, nest-sites, and landscape on the choice of habitat, (2) determine the major nest-site requirements, and (3) analyze to what extent habitat selection in the invaded area differs from that found in their native range.

STUDY AREA

The study was conducted in the city of Barcelona (NE Spain), excluding industrial areas and mountainous zones of the periphery (see Senar and Sol 1991). The study area (6,031 ha) was characterized by a predominance of urbanized habitat with some parks (582 ha) and a few residual woods. No ecologically similar birds occur in this area, and thus we assume that Monk Parakeet habitat selection was not constrained by competition with other species.

Factors influencing the choice of the habitat were studied at two spatial scales: (1) habitat selection within the city (macrohabitat selection) and (2) nest-site selection (microhabitat selection). To investigate microhabitat selection, two study sites in the overall study area were examined: Ciutadella Park (CIU) and Diagonal Avenue (DIA). CIU was a park (31 ha) with a high plant diversity, which was colonized by the species in 1975 (Batllori and Nos 1985). DIA was an urban area (7 ha), with four rows of palm trees regularly interspersed with *Platanus hybrida*. The first parakeets became established at DIA in 1991 and since then their number has increased dramatically.

METHODS

NEST LOCATION

The invasion of Monk Parakeets was monitored from 1992 to 1994 by prospecting the study area. When a new nest or a new chamber in a compound nest was found, it was plotted on a map and subsequently monitored. During the early summer of each year we carried out a survey of all nests and chambers in the study area. The number of nests increased during the three years of study due to both a growth in previous colonized areas and the colonization of new sites (D. Sol, unpubl. data).

MACROHABITAT SELECTION

Because the nest is the center of activity for the parakeets (Forshaw 1989; pers. observ.), and because in our study area feeding, roosting and social activities were often performed near the nests (Batllori and Nos 1985; pers. observ.), we divided the city into squares of 10 ha and used the presence of nests as an indication of suitable habitat within each square. The number of nests and chambers per square was assumed to be a reasonable estimate of the population density, although individuals per chamber varied from 0 to 4. This was more appropriate than estimating the population density by censuses, which presented many difficulties. Trees of all the early invaded zones of the study area (except the Montserrat Institute, see below) had been pruned recently, so we can reasonably assume the number of abandoned chambers was low. Moreover, abandoned nests were often recognized by their state of decay, so many of them were excluded from the analyzes.

Variables related to nest-sites, food availability and landscape structure (see Table 1) were measured at the squares containing nests in 1992 ($n = 21$), 1993 ($n = 27$), and 1994 ($n = 30$). Twenty-seven squares with no nests were selected at random and used to estimate the habitat available for the species.

In Spain, parakeet nests have been found in palms (*Phoenix* spp.), eucalyptus (*Eucalyptus* spp.), pines (*Pinus halepensis*), and elms (*Ulmus* spp.; Batllori and Nos 1985; pers. observ.). Thus, nest-site availability was estimated by counting the individuals of these four tree species in each square. Food available in each square was estimated through an index defined as the sum of plant species the parakeets had been observed feeding on, ranked in three categories: absent (coded 0), scarce (coded 1; 1–5 plants), or abundant (coded 2; >5 plants). Vegetable species included: *Phoenix* spp., *Cupressus* spp., *Egrostis* sp., *Populus* spp., *Taxus baccata, Robinia pseudoacacia, Platanus hybrida,* and *Ficus carica. Egrostis* was coded 0 (absent) or 1(present) due to the difficulty of using an equivalent criterion, so the index values fluctuated between 0 and 15.

MICROHABITAT SELECTION

Factors influencing nest-site selection were investigated at DIA and CIU study sites by comparing use and availability of nest trees. In both sites the species nested exclusively in palms. Variables describing aspects of the palms, surrounding vegetation (absent at DIA, so not measured) and human influences (Table 1) were

TABLE 1.   Variables characterizing the macrohabitat and microhabitat.

MACROHABITAT

NEST TREES: number of palms (*Phoenix* spp., PALMS), pines (*Pinus halepensis,* PINES), elms (*Ulmus* sp., ELMS), and eucalyptus (*Eucalyptus* sp., EUCAL) taller than 5 m[a].

DISTANCE PARK: distance from the center of the square to the nearest urban park (as is defined by the Council) (m).

PARK: percentage of garden park in the square (%).

FOOD: index of food abundance (0–17).

URBANIZED AREA: percentage of the square formed by houses and streets (%).

FOREST: percentage of the square formed by close woods (%).

SLOPE: slope of the square categorized as plane (0), weakly pendent (1), and pronounced pendent (2).

MICROHABITAT

HEIGHT: height of the palm trees from the ground to the bases of leaves (cm).

THICKNESS: diameter of the trunk at 1.5 m from the ground (cm).

FOLIAGE COVER: number of leaves counted from 5 m to the palm tree.

DISTANCE BUILDING: distance to the nearest building (m).

DISTANCE STICK TREE: distance to the nearest tree known to be used as stick supply for the nest (m).

OBSTRUCTING TREES: number of trees with their head contacting the palm tree foliage.

R10/R20 PALM TREES: number of palm trees counted in a 10 and 20-m radius around the palm tree.

R10/R20 STICK TREES: number of stick trees counted in a 10 and 20-m radius around the palm tree.

R10/R20 TREES: number of trees counted in a 10 and 20-m radius around the palm tree.

[a] Lowest height at which the species was found nesting.

measured in 1993 in 44 nests at DIA and 33 nests at CIU, and compared with those measured in 44 and 33 suitable random palms from each site, respectively. The inclusion of random trees that are not suitable nesting substrates would bias results by increasing the likelihood of showing preferences when none exist (Edwards and Collopy 1988). To reduce this bias, we only included in the analyses random trees that fell into the range of nest trees for each of the measured variables.

At the CIU site, the number of occupied palms during 1993 was only 17. However, in September 1993 some nests were removed by gardeners. Individuals built new nests both in the previously used palm trees and in new ones. We included these nests to increase the sample size. Therefore, occupied palm trees, whether containing nests before or after pruning ($n = 33$), were considered. To insure independence of data each occupied palm was considered only once.

STATISTICS

To test for nest-tree preferences, adjusted G-tests were used. To compare use and availability in both macrohabitat and microhabitat scales, we first performed a univariate analysis of the data using Student's t and Wilcoxon tests. Next, we used multivariate analyses. Variables non-normally distributed were log-transformed

and percentages were arcsine-transformed. For variables that could not be normalized, alternative statistical techniques were used (see below). Squared and cubed variables also were introduced into the multivariate analyses, but are only cited in the text when significant in the models.

On the macrohabitat scale, the squares containing nests were compared with random squares using a logistic regression analysis (LRA; see Donázar et al. 1993). This technique can be used to predict a binary dependent variable from a set of independent variables, and requires far fewer assumptions than the discriminant analysis. The response variable had the value 1 (squares with nests) or 0 (squares without nests). Linear multiple regression (LMR) was used to determine which of the macrohabitat variables influenced the number of nests and chambers per square. Since zero values also could affect the pattern observed (see Wiens 1991), they were tested in the models. Spatial analyses (D. Sol, unpubl. data) indicated that macrohabitat analyses were not significantly affected by the fact that the species was in process of colonizing the city, nor by social attraction in the choice of nest-site.

On the microhabitat scale, discriminant analysis (DA) was used to predict a binary dependent variable from a set of independent variables. Here, the assumptions of multivariate
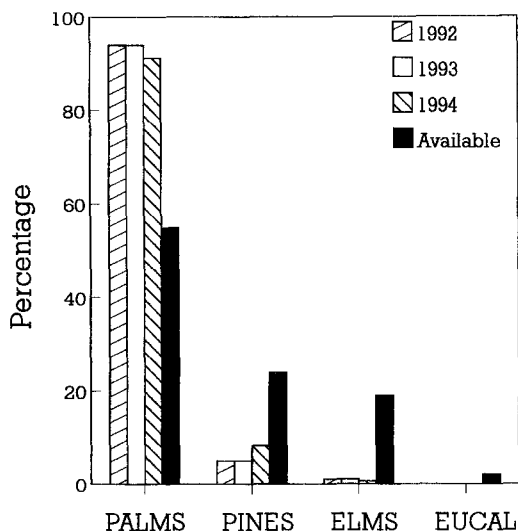
FIGURE 1.   Use and availability of nest tree species in the study area in 1992–1994.

normality of the independent variables and the equal variance-covariance matrices in the two groups were met. The response variable had the value 1 (used palm trees) or 0 (unused palm trees).

To construct the LRA and DA models, we tested all models resulting from the possible combinations of variables. Only variables improving the classification by more than 5% were included in each model. The models correctly classifying more than 75% of data were then retained. The robustness of the DA models were tested with a jack-knife procedure (see Donázar et al. 1993). LMR models were constructed through a modification of the stepwise proce-

dure, which involved testing the alternative models that were obtained when the second or the third most significant variable was included instead of the most significant one at each step (Donázar et al. 1993).

RESULTS

NESTING-TREE SPECIES

Most of the nests were located in palms, a few in pines, and the rest in a *Trachycarpus* sp., an elm, and on a wall covered by Ivy (*Hedera helix*) (Fig.1). To test whether the species preferred to nest in palms over the other tree species, we compared the use and availability of the main tree species in the study area (see Methods). Availability was measured as the percentage of individuals of each tree species in all the squares containing nests. The tree species used as nest-sites differed significantly from those available in the study area (Fig. 1); palms were used more often than expected and the other species less often (1992: $G_1 = 39.1$, $P < 0.001$; 1993: $G_1 = 105.2$, $P < 0.001$; 1994: $G_1 = 92.0$, $P < 0.001$). Similar results also were obtained in comparisons of use-availability between palms and pines (1992: $G_1 = 17.8$, $P < 0.001$; 1993: $G_1 = 64.3$, $P < 0.001$; 1994: $G_1 = 59.3$, $P < 0.001$).

MACROHABITAT SELECTION

There were significant differences between used and random squares (Table 2), the former tending to contain more palms and food, a higher percentage of park area, and to be located near urban parks. Squares containing forest areas were not used by parakeets. However, it is pos-

TABLE 2.   Mean (SE) of variables characterizing the squares where nests were located and random squares. Asterisks indicate statistical differences between used and random squares (Wilcoxon test).

| Variable | Used squares | | | Random squares |
	1992	1993	1994	
PALMS	19.57 (4.52)***	18.26 (3.65)***	17.63 (3.45)***	3.26 (1.53)
PINES	9.90 (2.72)	9.93 (2.19)	9.50 (2.09)	20.15 (11.82)
ELMS	4.90 (4.66)	3.85 (3.62)	3.47 (3.26)	12.37 (5.00)
EUCAL.	0.38 (0.21)	0.56 (0.29)	0.63 (0.26)	0.78 (0.67)
DIST. PARK	367.90 (79.75)*	378.70 (68.40)*	418.30 (65.9)	643.50 (88.83)
PARK	15.33 (2.89)**	12.97 (2.16)***	11.56 (1.98)*	6.23 (1.50)
FOOD	7.81 (0.67)**	7.81 (0.60)***	8.33 (0.44)***	5.52 (0.44)
URBAN. AREA	85.74 (6.38)	87.88 (5.04)	89.67 (4.58)	89.67 (7.42)
FOREST	0.00 (0.00)	0.00 (0.00)*	0.00 (0.00)*	2.32 (1.71)
SLOPE	1.14 (0.16)	1.15 (0.14)	1.17 (0.13)	1.04 (0.16)
n	21	27	30	27

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 3.   Best logistic regression models comparing squares with nests (value of the response variable = 1) and without nests (value = 0). Independent variables were all the macrohabitat variables (see Table 1).

Year	MODEL	Parameter estimate	SE	P	R	% correctly classified
1992	PALMS	0.11	0.04	0.01	0.27	77
1993	PALMS	0.12	0.05	0.01	0.25	76
1993	PALMS	0.11	0.04	0.01	0.24	81
	DIST. PARK	−0.00	0.01	0.17	0.00	
1994	PALMS	0.27	0.10	0.01	0.25	76
1994	PALMS	0.27	0.10	0.01	0.26	86
	SLOPE	0.53	0.47	0.27	0.00	
1994	PALMS	0.19	0.09	0.04	1.78	84
	FOOD	0.32	0.19	0.09	1.08	

sible that some of the variables differed between used and random squares simply because of their correlation with other variables. For instance, food availability was correlated with the number of palms (Spearman rank correlation: $r_s = 0.63$, $P < 0.001$, $n = 55$) and with park area ($r_s = 0.47$, $P < 0.001$, $n = 55$), although the two last variables showed a low but significant correlation ($r_s = 0.29$, $P = 0.03$, $n = 55$). Therefore, logistic regressions were used to describe major differences between used and random squares. The number of palms per square was the only variable included in all the models, and it showed the highest R-values (Table 3).

The most important factor influencing the density of nests and chambers in 1993 and 1994 was the number of palms in the square (Table 4). Several other variables also were introduced in some models, but their contributions to the variance were lower. In 1992, the variance of data cannot be explained accurately by any predictors; variables with significance in the model were found only for two of the four models. The

relationship between the number of nests and palms was strong in 1993 and 1994 (Pearson's product-moment correlation: $r = 0.74$, df = 26, $P < 0.001$; $r = 0.76$, df = 29, $P < 0.001$, respectively), but lower in 1992 ($r = 0.55$, df = 20, $P = 0.01$; Fig 2.), suggesting an infrautilization of nest-sites in 1992. However, an outlier (the Institute Montserrat square) greatly influenced the regression lines (especially in 1992) (see Fig. 2). This was one of the first areas colonized by parakeets (Batllori and Nos 1985) and it already appeared to be saturated.

MICROHABITAT SELECTION

Used and unused random palms showed significant differences within the study sites. In both sites, the mean height of palms was greater for used than random trees (unpaired t-test, $P < 0.001$). Used trees also differed from unused trees in thickness (only at DIA; $t_{87} = 2.53$, $P = 0.01$) and in foliage cover (only at CIU; $t_{65} = 3.67$, $P < 0.001$), although such differences could have appeared from their correla-

TABLE 4.   Multiple regression equations used to predict which variables of the macrohabitat (Table 1) affected the density of nests and chambers in each year (NESTS = nests per square, NESTS + ZEROS = zeros also included, CHAMBER = Chambers per square, CHAMBER + ZEROS = zeros also included).

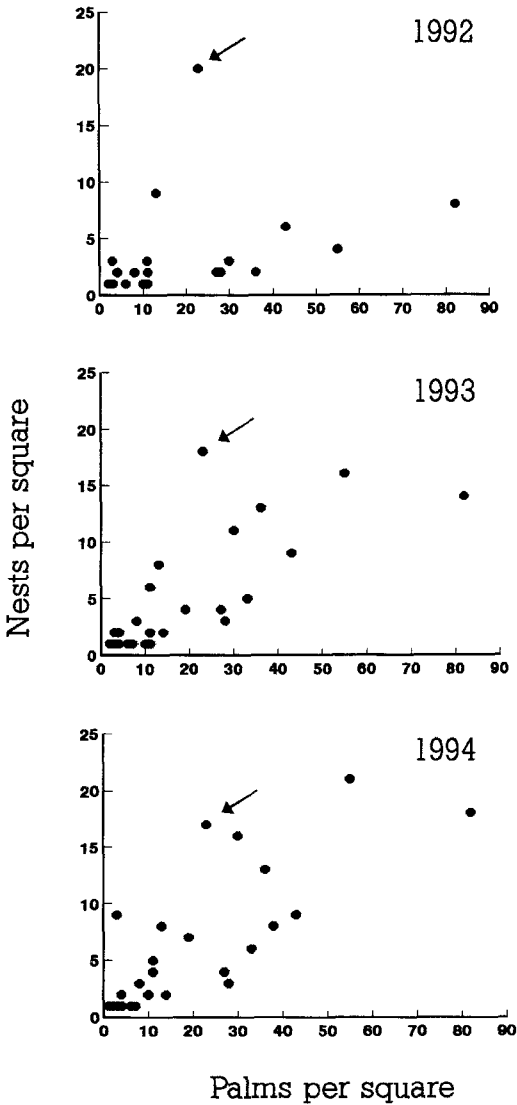| Year	Dependent variable	Independent variable	Coefficients (SE)	P <	df	Cumulative adjusted R^2
1992	NESTS + ZEROS	PALMS	0.10 (0.03)	0.001	46	0.23
	CHAMBER	PINES	0.68 (0.28)	0.05	19	0.35
1993	NESTS	PALMS	0.18 (0.04)	0.001	25	0.44
	NESTS + ZEROS	PALMS	0.19 (0.03)	0.001	52	0.49
	CHAMBER	PALMS	0.56 (0.15)	0.001	25	0.35
	CHAMBER + ZEROS	PALMS	0.59 (0.09)	0.001	52	0.42
1994	NESTS	PALMS	0.29 (0.04)	0.001	27	0.62
		FOOD	−0.66 (0.30)	0.05		0.66
	NESTS + ZEROS	PALMS	0.26 (0.02)	0.001	53	0.69
	CHAMBER	PALMS	0.61 (0.14)	0.001	28	0.40
	CHAMBER + ZEROS	PALMS	0.70 (0.09)	0.001	53	0.52

FIGURE 2. Relationship between the number of nests and the quantity of palm trees per square in the three years of study. Arrows mark the square corresponding to the Montserrat Institute (see text).

TABLE 5. DA models comparing used and random palm trees at DIA and CIU study sites (data from 1993).

	DIA	CIU	
Canonical correlation	0.57	0.52	0.48
Wilks' lambda	0.68	0.73	0.77
Chi-square value	33.5	20.1	16.3
Correctly classified	78	75	76
Significance level	<0.001	<0.001	<0.001
DA function-variable correlation			
HEIGHT	1.000	0.85	0.96
THICKNESS	—	0.34	—
OBSTRUCTING TREES	—	—	−0.49

lected by parakeets decreased with the increase in parakeet population density ($F_{2,54} = 3.41$, $P < 0.05$).

At CIU, the height of palms also was the variable with the greatest influence on the discriminant model, with the highest discriminant function-variable correlation and standardized coefficient (Table 5). The two resulting models, however, also included the variables THICKNESS and OBSTRUCTING TREES. The jack-knife classifications differed from the models by less than 2%, also indicating the robustness of the models.

Results from the two study sites indicate the height of palms have the most influence on choice of nest-site. However, results from CIU appeared more confusing than those from DIA. One reason could be that CIU had been colonized by the species a long time ago, so our data may reflect a pattern (nest-site use) rather than a process (selection; see Wiens 1991 for a discussion of this topic). However, the greater complexity in habitat structure at CIU than at DIA or other unknown factors also could have affected the results.

DISCUSSION

The Monk Parakeet exhibited great selectivity in habitat choice. The species inhabited parks with palms present and which offered a great abundance of plants for foraging. However, food apparently exerted little influence on parakeet density. This may be the result of the generalist foraging behavior of the species (Freeland 1973, Batllori and Nos 1985, Bucher et al. 1990, Hyman and Pruett-Jones 1995), the presence of many parks in the area, and the fact that

tion with height. Discriminant analyses were used to describe major differences among these groups (Table 5). At DIA, the height of the tree was the unique variable entering into the discriminant function, correctly classifying 78% of observations. The jack-knife procedure exhibited a very similar percentage of observations correctly classified (also 78%), indicating the robustness of the model. The comparison between years showed that the height of palms se-

parakeets may forage far from their nests (de Schaetzen and Jacob 1985, Hyman and Pruett-Jones 1995). In Barcelona, the distance from nests to the nearest urban park averaged less than 500 m, indicating that parakeets did not need to travel great distances to meet their daily energy requirements.

On the other hand, palms represented the preferred substrate for nesting, and most nests were located in this tree species. The number of palms was the main factor influencing population density, suggesting that the choice of habitat was based primarily on finding a suitable nest-site. The tendency of the species in South America to expand into new areas whenever nest-sites become available also supports this idea (Bucher and Martin 1987, Forshaw 1989). However, it seems unlikely that the size of the parakeet population in Barcelona is limited by the number of palms, because the species is able to nest in many other tree species and structures.

A preference by Monk Parakeets for nesting in palms whenever available also has been observed in Argentina (E. Bucher, pers. comm.). The preference for palms cannot be attributed to a lack of other suitable tree species for nesting, because tall eucalyptus, pines and other apparently favorable trees also were available in the city. In some areas of Barcelona, for instance, parakeets preferred to nest in lower palms rather than in taller eucalyptus and pines. The specialization for palms as nesting substrates may be related to certain characteristics of palms. For instance, terrestrial predators (e.g., cats) may find palms difficult to climb. Palms could facilitate the construction and maintenance of the nest, especially important for inexperienced juveniles. Nests in palms were located on the base of the leaves, providing good points of anchorage for the sticks, and probably requiring less material and building effort than with other types of trees. Moreover, the top of the tree, formed like an umbrella, could provide cover from the rain and wind throughout the year, reducing the time and energy required for nest maintenance.

Parakeets exhibited a consistent tendency to nest in the tallest palms available, although other factors also can affect the final choice. In Córdoba (Argentina), individuals also preferred to nest in eucalyptus and other tall trees or human structures rather than lower native vegetation (Navarro et al. 1992). This could be a way

to reduce predation risk (see Tomialojc 1978, Osborne and Osborne 1980, Li and Martin 1991). The nest of Monk Parakeets may be more susceptible to predation than nests in tree or cliff cavities (Navarro and Bucher 1990, Navarro et al. 1992), so safety from predators is expected to exert a great influence on selection of the nest-site.

Although the Monk Parakeet is a nest-site generalist in its native range (Forshaw 1989), our results indicate that in the first stages of colonization the species may behave as a specialist (see Hildén 1965 for additional examples). This nest-site specificity may have resulted from an innate response to certain proximal cues of the habitat. Thus, the inherent advantages of nesting in palms could have led to specialization for this tree species. However, it also is possible that the particular characteristics of the area (i.e., an urban habitat of recent invasion) can have accentuated the specificity of the choice. For example, the high level of human disturbance in urban areas could have enhanced the tendency of parakeets to select the more protected nest-sites.

However, according to current models of habitat selection (reviewed in Block and Brennan 1993), it is probable that a species becomes more generalist in nest-site choice as their population expands and less nest sites remain available. The observation that parakeets used lower palms after the taller palms became occupied is consistent with this interpretation. Future research must determine to what extent the species is able to use other types of nesting structures.

MANAGEMENT IMPLICATIONS

The Monk Parakeet population in Barcelona may be a source population from which birds disperse to surrounding nonurban areas (see Clavell et al. 1991) where the species could become an agricultural pest and, more importantly, have a strong impact on the native biota (see Drake et al. 1989, Lodge 1993). These potential problems demand immediate preventive actions. Our finding that securing a nest-site is a key factor in the parakeets' habitat selection has important implications for species management, because it suggests that we could limit population density by limiting the number of available nest-sites. However, the simple destruction of nests is not an efficient measure of control be-

cause birds return to build their nests in a couple of days (pers. observ.). It would be necessary to develop alternative strategies, such as physical barriers, to limit nest-site availability.

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