ORNITOLOGIA NEOTROPICAL 4: 43–54, 1993

NATURAL RANGE EXPANSION AND LOCAL EXTIRPATION OF AN EXOTIC PSITTACINE — AN UNSUCCESSFUL COLONIZATION ATTEMPT

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Resumen. El Perico Cara Sucia *Aratinga pertinax* es oriundo de Panamá, norte de Suramérica e islas al norte de la costa venezolana. Se cree que este perico fue introducido a Santo Tomás, Islas Vírgenes, desde Curazao antes de los mediados del siglo XIX, aunque no existen registros para indicar cuando y como esto pudo haber ocurrido. El perico no se había reportado para la isla de Puerto Rico, Vieques o Culebra antes de 1975. Sin embargo, en ese año *A. pertinax* sostuvo una aparente expansión natural en su distribución de Santo Tomás a cada una de estas localidades. Desde su descubrimiento en abril de 1975 las 5 aves de la población del este de Puerto Rico anidaron unas 5 veces y produjeron unos 11 pichones que volaron. La población creció a un máximo de 10 pájaros en junio de 1979 pero para julio de 1980 sólo quedaba un pájaro y la población ya no existía al comienzo de lo que hubiera sido la época reproductiva de 1982. La poblaciones en las islas de Culebra y Vieques aparentemente fueron extirpadas antes de 1976. Las pérdidas en la población del este de Puerto Rico fueron bajas durante los primeros cuatro años de la colonización, cuando la reproducción fue adecuada y la mortandad baja. En contraste, entre 1978 y el tiempo de la desaparición de la población en 1982, la extirpación esperada fue de 0.999. Se describen el uso del hábitat, comportamiento general, biología reproductiva, competidores y depredadores de la población del este de Puerto Rico. Se discuten implicaciones biogeográficas, evolutivas y conservacionistas.

Abstract. The Brown-throated Parakeet *Aratinga pertinax* is native to Panama, northern South America, and the islands off the northern coast of Venezuela. It is widely believed that the parakeet was introduced to St. Thomas, Virgin Islands, from Curaçao before the mid-19th century, although no records exist as to when and how this may have occurred. The parakeet was not recorded from Vieques or Culebra islands or mainland Puerto Rico before 1975. However, in that year *A. pertinax* underwent an apparent natural range expansion from St. Thomas into each of these sites. The 5 birds in the eastern Puerto Rico population made 5 breeding attempts and fledged 11 young since their discovery in April 1975. That population grew to a maximum size of 10 birds in June 1979. However there was only 1 bird left by July 1980, and the population no longer existed at the beginning of what would have been the 1982 breeding season. The populations on Culebra and Vieques islands were apparently extirpated by 1976. Losses in the eastern Puerto Rico population were low during the first four years of colonization, when reproduction was adequate and the mortality was low. However, between 1978 and the time of population disappearance in 1982, the expected extirpation was 0.999. Habitat use, general behavior, breeding biology, competitors and predators of the colonizing population in eastern Puerto Rico are described. Biogeographic, evolutionary, and conservation implications of these observations are discussed. *Accepted 7 September 1992.*

Key words: Aratinga pertinax, *breeding biology, Brown-throated Parakeet, Caribbean, colonization, Culebra Island, Curaçao, extinction, extirpation, parakeet, Puerto Rico, range expansion, St. John, St. Thomas, Tortola, Vieques Island, Virgin Islands, West Indies.*

INTRODUCTION

Source populations of colonizing species are usually abundant and widespread in the origin locality. Immigrants to islands can initially appear to be excellent competitors and may exhibit ecological release: their populations increase greatly and spread into habitats not occupied by the parent population (MacArthur & Wilson 1963, 1967; Cox & Ricklefs 1977). Furthermore, invading populations may be able to exploit niches not occupied by native species. After the invaders become established, however, their competitive ability appears to wane, then distribution among habitats becomes restricted, and local population density decreases. These trends may eventually lead to extirpation. Furthermore, the probability of extirpation in-

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creases as population size decreases (MacArthur & Wilson 1967, Pielou 1969). Extirpation of small local populations may occur when local climatic conditions become severe, when an efficient predator is introduced into the community, or as a result of competition with ecologically similar species (DeBach 1966, Ricklefs 1979). Colonizing populations on small islands are particularly vulnerable to extirpation because they are restricted geographically and are infrequently augmented by immigration.

I observed an incipient colonization of several West Indian islands by an exotic psittacine, the Brown-throated Parakeet, *Aratinga pertinax*. The species is native to Panama, northern South America, and islands off the northern coast of Venezuela (including Curaçao, Bonaire, and Aruba of the Netherlands Antilles; American Ornithologists' Union 1983, Forshaw 1989). The parakeet was recently introduced to Dominica, formerly occurred on Martinique (now extirpated), and persists in St. Thomas, U.S. Virgin Islands (Clark 1905, Norton 1983, Forshaw 1989). Marien & Koopman (1955) suggested three possible scenarios for the source of the disjunct population of *Aratinga pertinax* in St. Thomas: (1) introduction by humans, (2) direct natural overwater transportation, perhaps storm-aided, and (3) natural range extension by island-hopping through the Lesser Antilles, followed by local extirpations. Most authorities favor the hypothesis that the species was introduced by man (Graf von Berlepsch *in* Hartert 1893, Marien & Koopman 1955, Leopold 1963).

I review the status of *A. pertinax* in St. Thomas and other Virgin Islands, and I report on a recent unsuccessful attempt at colonizing the nearby islands of Vieques, Culebra, and Puerto Rico. I use these data to discuss the origin of the St. Thomas population and possible biogeographical, ecological, and conservation implications for other species of West Indian parakeets.

HABITATS VISITED

I observed parakeets in subtropical moist and subtropical dry forests of eastern and western St. Thomas during 31 May—3 June 1977, and July of both 1978 and 1979. I visited Culebra Island (2,730 ha, Fig. 1) as follows: 30 October—1 November 1974, 19—21 February 1975, 22—23 April 1975, 8—9 November 1977, 18—19 July 1978, 31 July—1 August 1978, and 20—23 June 1980. Culebra Island is 27 km northeast of Puerto Rico and 25 km west of St. Thomas. The natural vegetation is subtropical dry forest (Ewel & Whitmore 1973).

I visited Vieques Island (13,766 ha, Fig. 1) on 30 October 1974, 19 February 1975, 22 April 1975, 8 November 1977, 18 July 1978, 31 July 1978, 14 October 1978, and 31 October 1978. Vieques Island lies 9.7 km east of Puerto Rico and 35 km southwest of St. Thomas. The vegetation of Vieques Island is classified as subtropical dry forest and subtropical moist forest (Ewel & Whitmore 1973).

The Roosevelt Roads Naval Station (3,260 ha, Fig. 1) is within the subtropical dry forest zone (Ewel & Whitmore 1973) of easternmost Puerto Rico and is characterized by salt pannes and mangrove forests in the lowlands (dominated by Black Mangrove *Avicennia germinans*, Red Mangrove *Rhizophora mangle*, White Mangrove *Laguncularia racemosa*, Button Mangrove *Conocarpus erectus*) and scrub dominated by the exotic leadtree *Leucaena leucocephala* in the dry areas (Wiley & Wiley 1979). Hardwood canyon forests, dominated by Royal Palm *Roystonea borinquena*, Red Manjack *Cordia nitida*, Mango *Mangifera indica*, and Shortleaf Fig *Ficus citrifolia*, lead into the mangrove bottoms. I visited the Roosevelt Roads Naval Station at least each 2—3 days from March through July in 1974—1975 and again in 1977—1981, and at 1—2 week intervals during August—February in 1974—1978 and in 1980—1981. I continued to visit the Roosevelt Roads study area at least every other week from 1982 through 1986.

OBSERVATIONS AT NESTS

Observations of breeding parakeets were made from blinds placed on the ground or in a tree about 10 m from the nest. Individual birds were identifiable in the short term (i.e., seasonally) by molt and in the long-term (year to year) by facial plumage and color of soft parts. Nine chicks (3 in 1978, 6 in 1979) were marked with stainless steel leg bands. At four nests I installed a door

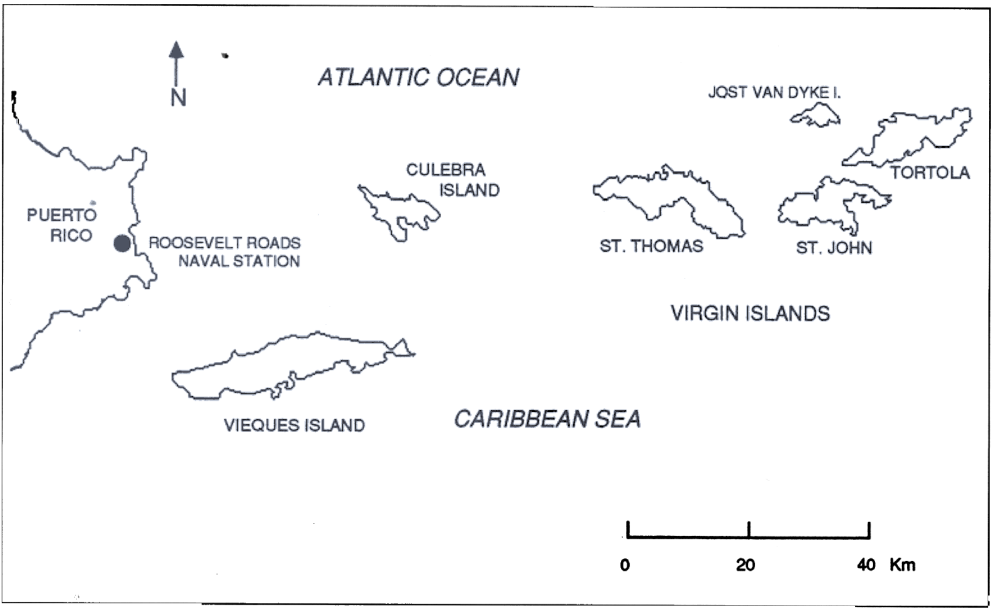

FIG. 1. Northwestern Virgin Islands, Culebra Island, Vieques Island, and eastern Puerto Rico.

large enough to allow access to the nest chamber for regular inspections. Nests were inspected for contents at one-week intervals until about one week before chicks fledged. Nests were not inspected again until about one week after the youngest chick was expected to fledge. Fledging was assumed if chicks reached the full-feathered stage and no chick remains or other evidence of predation were found in the nest chamber.

NEST SITE AVAILABILITY

At Roosevelt Roads, I surveyed habitat for parakeet nest cavities in 1.64 ha of white and black mangrove-dominated forests and adjacent hardwood canyon forest. Characteristics of trees containing *A. pertinax* nest cavities were determined from active nests and from published records and unpublished data in museum collections of eggs. From these data, I derived the following conservative measurements, which I used in my surveys of nest site availability: diameter at breast height (dbh) of nest cavity-bearing tree —≧40 cm, height of cavity above ground —3 m, diameter cavity entrance —7.0 cm, interior chamber diameter —20 cm, cavity depth —40 cm.

The minimum diameter of a termitarium was based on observations of active termite nests used by *A. pertinax* in St. Thomas and Puerto Rico and from unpublished data on the similar-sized Hispaniolan Parakeet (*A. chloroptera*, length —32 cm versus 25 cm for *A. pertinax*) in Hispaniola and Orange-fronted Parakeet (*A. canicularis*, length —24 cm) in Guatemala (Wiley, unpubl. data). From these observations, I judged the minimum diameter of a termitarium suitable for a parakeet nest to be 55 cm, the minimum dbh of a termitarium-bearing tree to be 20 cm, and the minimum height above the ground of a suitable cavity 3 m.

Trees of suitable size were searched for cavities from the ground or, if sections of the trunk were not visible from that perspective, by climbing. All cavities were inspected while climbing the trees.

CALCULATIONS

Expected extirpation rates ($P_{[0]}$) of the population were calculated following Pielou's (1969) formula. I followed Ricklefs (1979) in determining feeding niche overlap among species.

STATUS AND POPULATION CHANGES ON ST. THOMAS AND OTHER VIRGIN ISLANDS

Because of morphological resemblances, most authorities have considered the St. Thomas population of *A. pertinax* to represent the same race as is endemic to Curaçao, *A. p. pertimax* (Hartert 1893, von Berlepsch *in* Hartert 1893, Ridgway 1916, Wetmore 1927, Leopold 1963, Forshaw 1989; but see Marien & Koopman 1955). If the parakeet has been introduced to St. Thomas, it must have been before the mid-nineteenth century, for several naturalists reported parakeets (probably *A. pertinax*) in St. Thomas during that period (Ledru 1810, Knox 1852, Newton 1859, Sclater 1859). The earliest known specimen from the Virgin Islands was collected in 1860 (Forshaw 1989).

Although generally regarded as common on St. Thomas from the mid-nineteenth century through the early part of the twentieth century, the Brown-throated Parakeet population underwent substantial fluctuations in numbers, including near-extirpation by the hurricanes of 1926 and 1928 (Knox 1852, Newton & Newton 1859, Eggers 1878, Hartert 1893, Nicoll 1904, Mortensen [1909] *in* Wetmore 1927, Nichols 1943). It subsequently increased in numbers but, like before the 1926 and 1928 storms, remained largely confined to the eastern half of the island (Nichols 1943). By the early 1960s, the parakeet had extended its range to most parts of St. Thomas, and the population was estimated at about 400 birds (Leopold 1963). Murray (1969) reported it as a common resident nesting on St. Thomas. In recent years, it has also been recorded from St. John (3.8 km east of St. Thomas, Fig. 1), where apparently it has not become established (American Ornithologists' Union 1983, Raffaele 1983, Norton 1985; Fig. 1). Mirechi *et al.* (1977) reported that occasionally groups of *A. pertinax* strayed from St. Thomas to Tortola 15 km northeast of St. Thomas (Fig. 1) and that possibly a small flock resided there.

SPREAD OF THE PARAKEET TO PUERTO RICO'S EASTERN SATELLITES

The Brown-throated Parakeet was not previously recorded from Vieques or Culebra islands (e.g., Wetmore 1916a, 1916b, 1917, 1927; Sorrie 1975; Kepler & Kepler 1978). However, Gundlach (1878) heard of parakeets (species unknown) on Vieques and Wetmore (1916a, 1916b) was told they sometimes were seen on that island in the June to August rainy season. Sorrie (1975) did not find them on Vieques Island during his work from June 1970 to July 1971, nor did colleagues and I detect the parakeet during surveys of Vieques and Culebra in 1974. However, on 22 April 1975 I found 3—7 *A. pertinax* at Ensenada Honda (Yanuel Lagoon) and 12 unidentified parakeets near Puerto Ferro, Vieques. J. Declet (*in* Pérez-Rivera & Vélez 1980) also observed Brown-throated Parakeets in Vieques Island.

On Culebra Island, several contemporary observations were made of unidentified parakeets. Cameron Kepler (pers. comm.) was told by a Culebra resident that parakeets (*Aratinga chloroptera*?) had regularly visited Cayo Norte to feed on *Coccoloba uvifera* in December for several years in the late 1960s and early 1970s. Herbert Raffaele (pers. comm.) was told of a flock of parakeets (species unknown) at Playa Larga in Culebra in 1972. A Culebra resident also told Raffaele of a flock of about 8 parakeets at Playa Grande on 31 May 1972. I observed *Aratinga pertinax* in the forested hillsides northeast of Playa Flamenco on Culebra Island on 21 February 1975, when I estimated a population of 4—8 individuals. On 23 April 1975, I saw a flock of 25 *A. pertinax* at Playa Grande on Culebra Island.

I did not find *pertinax* on either island during visits in subsequent years, nor were other reports of the parakeet made after 1975 (Duffield & Cardona 1978, Furniss & Collazo 1983, Marc Weitzel, pers. comm.).

HISTORY OF *ARATINGA PERTINAX* COLONIZATION OF EASTERN PUERTO RICO

Historically, *Aratinga pertinax* was not confirmed from Puerto Rico (Chaplain 1859, Wetmore 1916a, 1927), although Chaplain (1859) noted parakeets there, which Clark presumed were introduced Brown-throated Parakeets from Curaçao. Sorrie (pers. comm.) did not find *Aratinga pertinax* on the Roosevelt Roads Naval Station during his residence there from November 1969 to August 1971. I also did not find the

TABLE 1. Population data for *Aratinga pertinax* in the Roosevelt Roads Naval Station, Puerto Rico, 1973—1982.

Year	Pairs	Nonpaired individuals	Breeding attempts	Chicks fledged	Prebreeding population	At end of breeding season	Minimum postbreeding population	Disappeared during breeding season	Disappeared during postbreeding season
1973	0	0	—	—	—	—	—	—	—
1974	0	0	—	—	—	—	—	—	—
1975	2	1	0	—	5	5	3	0	2
1976	1	1	0	—	3	3	3	0	0
1977	1	1	1	2	3	5	5	0	0
1978	1	3	1	3	5	7	7	1	0
1979	2	3	2	6	7	10	6	3	4
1980	1	4	1	0	6	4	1	2	3
1981	0	1	—	—	1	1	0	0	1
1982-86	0	0	—	—	0	0	0	—	—
Totals				11				6	10

parakeet there during extensive field work in 1974 and early 1975. Mary Hickman (pers. comm), a Base resident and avid bird watcher, first observed the parakeet at Roosevelt Roads in April 1975. The population at that time consisted of a minimum of 5 individuals (2 pairs and 1 single), but grew to a maximum size of 10 birds in June 1979 (Table 1). I found no evidence of additional immigration into the area after 1975. Eleven chicks fledged from five known nesting attempts, but the young birds suffered high mortality during their first year (Table 1). The population declined to 1 bird by July 1980, and was extirpated by the beginning of the 1982 breeding season (Table 1).

Expected extirpation rate of the population ($P_{[0]}$) was low during the first years of the colonization when reproduction was good and mortality was low (Fig. 2). However, thereafter $P_{[0]}$ quickly approached unity ($xP_{[0]}$ 1979—1980 = 0.999).

HABITAT USE OF THE COLONIZING POPULATION

Aratinga pertinax uses a wide variety of habitat types rangewide, including mangroves, savannahs, open woodland, dry thorn and cactus scrublands, cultivated farmlands, fruit plantations, and gardens (Lowe 1907, Haverschmidt 1968, Wetmore 1968, Meyer de Schauensee 1970, Voous 1983). The Curaçao race is found in virtually all of that island's habitats, but particularly in fruit plantations, manchineel (*Hippomane mancinella*) thickets, mangroves, and semi-deserts with cactus and acacias (Voous 1983). In St. Thomas, the parakeet prefers wooded thickets in the hills, although it descends at times to feed on fruits in the lowlands (Nichols 1943, Raffaele 1983, pers. obs.). Norton (*in* Raffaele 1983) reported it as uncommon in mangrove habitat on St. Thomas. Habitat use by the parakeet in Puerto Rico and its satellites was similar to that in St. Thomas. Parakeets were observed in mangrove forests and open woodlands on hillsides on Culebra Island, mangrove forest edge and open scrub on Vieques Island, and mangrove forest and adjacent hardwood canyon-leadtree scrub edge in eastern Puerto Rico. Parakeets roosted

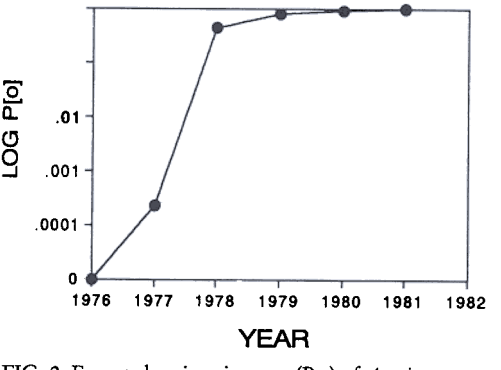

FIG. 2. Expected extirpation rate ($P_{[0]}$) of *Aratinga pertinax* population at Roosevelt Roads Naval Station, eastern Puerto Rico, 1975—1981.

and nested primarily in the mangrove forest, but foraged in adjacent canyons and, occasionally, suburban areas.

GENERAL ECOLOGY AND BEHAVIOR

Aratinga pertinax feeds and roosts in pairs or small to large flocks (Wetmore 1968, Voous 1983, Forshaw 1989). The parakeet is a food generalist, feeding on a variety of seeds, fruits, nuts, blossoms, and possibly insects and their larvae (Hartert 1893, Voous 1983, Forshaw 1989). It shows no definite breeding season in most parts of its range (Schäfer & Phelps 1954, Haverschmidt 1968, Wetmore 1968). *Aratinga pertinax* on Curaçao has been reported as breeding throughout the year, but primarily following a rainy period (Voous 1957, 1983). On St. Thomas, a bird collected on 22 March 1892 had an egg in its oviduct, and Nichols (1943) took 2 eggs from a nest on 23 March (in collection of Western Foundation of Vertebrate Zoology, Los Angeles).

Breeding pairs are usually dispersed, but birds have been reported nesting in small colonies of up to seven pairs (Voous 1957). *Aratinga pertinax* nests in holes, often excavated by the birds in decayed trunks of date palms, in earthen and sand walls, and in crevices and holes in rock (Hartert 1893, Voous 1983, Forshaw 1989). Most frequently, nesting holes are dug in large tree nests of termites (Myers 1935, Hindwood 1959). Nests of Brown-throated Parakeets using termitaria in the Netherlands Antilles had an entrance tunnel of up to 50 cm in length and 7—10 cm in width, with a nest chamber of 25 cm in diameter and 15 cm in height (Voous 1983). In St. Thomas, Nichols (1943) reported a nest burrow about 1 m deep in a live termite nest, 5.5 m from the ground. Clutch size is generally reported as 4—7 eggs (Forshaw 1989).

BREEDING BIOLOGY IN EASTERN PUERTO RICO

Chronology. I found 5 nests in eastern Puerto Rico from 1977 to 1980 (Table 2). Nests contained eggs in mid-March through late April, which coincides with the onset of the rainy season in eastern Puerto Rico (Wiley & Wiley 1979). Chicks fledged from mid-May to late June and loosely associated with adults at least until the next breeding season.

Nest Site Characteristics. Four of the five parakeet nests were in active termitaria of *Nasutitermes costalis* in trees at the inland edge of white mangrove-dominated forest and in a narrow hardwood canyon. The insects sealed off the birds' breeding chamber with layers of cellulose, but I observed no other obvious interactions between the birds and termites. One of the termitaria nests was in a Mango (*Mangifera indica*), two were in White Mangroves, and another was in a Black Mangrove (Table 2). The fifth nest was 11.9 m high in the broken trunk of a dead Royal Palm (*Roystonea borinquena*). Entrances of nests in termitaria averaged 9.8 ± 1.71 (S.D., Range = 8—12) cm in diameter and 5.3 ± 1.13 (R = 4.3—6.9) m above the ground (Table 3). Nest chambers averaged 57.0 ± 14.58 (R = 40—75)

TABLE 2. Productivity of *Aratinga pertinax* at the Roosevelt Roads Naval Station, eastern Puerto Rico, 1977—1980.

Nest no. (Habitat description and nest tree)	Number			
	Eggs[a]	Hatchlings	Older chicks	Fledglings[b]
1 (Canyon-Mango)	5	4	2	2
2 (Canyon-Royal Palm)	5	5	3	
3 (Mangrove forest-White Mangrove)	7	5	4	
4 (Mangrove forest-White Mangrove)	4	4	4	
5 (Mangrove forest-Black Mangrove)	6	0	—	
Totals	27	18		11
	5.4 ± 1.14	3.6 ± 2.07	2.6 ± 1.67	2.2 ± .30

[a] All eggs were fertile. [b] Nests were not watched through fledging. Fledging was assumed if chicks reached the completely feathered stage (i.e., within 1 week of fledging), and no chick remains or evidence of predation were found in the nest chamber.

TABLE 3. Dimensions of *Aratinga pertinax* nest cavities in termitaria and a Royal Palm, Roosevelt Roads Naval Station, eastern Puerto Rico, 1977—1980.

Nest number	Height above ground (m)	Nest chamber		
		Entrance diameter (cm)	Inside	
			diameter (cm)	depth (cm)
Nest sites in termitaria				
1	5.3	10	25	75
3	4.8	9	27	40
4	4.3	12	23	60
5	6.9	8	27	53
Mean ± SD	5.3 ± 1.1	9.8 ±	25.5 ± 1.91	57.0 ± 14.58
Nest site in dead Royal Palm				
2	11.9	48	40	92
All nest sites				
Mean ± SD	6.6 ± 3.10	17.4 ± 17.17	28.4 ± 6.69	64.0 ± 20.11

cm deep and 25.5 ± 1.91 (R = 23—27) cm inside diameter. I observed *A. pertinax* modifying the termitaria cavities, but did not see birds selecting or initiating excavation of the cavities.

Cavity Availability. Of the 164 suitably sized (dbh ≧ 0.40 m) trees in 1.64 ha surveyed at Roosevelt Roads, only 5.5% (n = 9) contained cavities of adequate dimensions for nesting parakeets. Of these cavities, 56% (n = 5) were at heights (≧ 3 m) suitable for parakeet nests. Tree-borne termitaria were more common than suitable cavities; 11.5% of larger trees (dbh ≧ 20 cm; n = 1,844) had full-sized termitaria (i.e., minimum 55 cm diameter). Of these termitaria, 79% (n = 168) were at a height suitable for nesting parakeets.

Productivity and Nest Success of the Colonizing Population. Clutches at Roosevelt Roads averaged 5.4 ± 1.14 (R = 4—7) eggs, all of which were fertile, 66.7% hatched, and 40.7% fledged (Table 2). Of those nests that hatched eggs, broods averaged 4.5 ± 0.58 (R = 4—5) first-week chicks; 3.3 ± 0.96 (R = 2—4) chicks survived to the mid-nestling period; and 2.8 ± 0.50 (R = 2—3) chicks fledged (i.e., at least reached the last week of the brooding period).

One of the five nests in eastern Puerto Rico failed, apparently after the adults deserted for undetermined causes. All other nests were successful. Pearly-eyed Thrashers (*Margarops fuscatus*) are aggressive predators of the eggs and young chicks of cavity-nesting birds (Snyder *et al.* 1987). Thrashers were observed on the termitaria used by the parakeets, but they only perched momentarily and made no attempt to enter the cavities.

FOOD HABITS

In Puerto Rico, I observed *Aratinga pertinax* feeding on fruits and seeds of 14 plant species, especially Mango, Red Manjack, Royal Palm, Brisselet (*Erythroxylum rotundifolium*), Florida Boxwood (*Schaefferia frutescens*), Coco Plum (*Chrysobalanus icaco*), Mountain Immortale (*Erythrina poeppigiana*), and Short-leaf Fig (Table 4). Voous (1957) reported that crop and stomach

TABLE 4. Food items observed being eaten by *Aratinga pertinax* at Roosevelt Roads Naval Station, eastern Puerto Rico, 1975—1981.

Food species	No. observations	% observations
Mangifera indica		
Cordia nitida		
Roystonea borinquena		
Erythroxylum rotundifolium		
Schaefferia frutescens		
Chrysobalanus icaco		
Erythrina poeppigiana		
Ficus citrifolia		
Avicennia germinans		
Coccoloba unifera		
Prosopis juliflora		
Tamarindus indica		
Annona muricata		
Citus aurantium		

contents of birds collected in the Netherland Antilles were comprised of fruits and seeds; *Caesalpinia*, *Acacia*, *Prosopis*, and Organ Pipe Cactus (*Cereus repandus*) were the most numerous. Birds were also seen eating the fruits of *Malpighia* and flowers of *Gliricidia sepium* (Voous 1957).

POTENTIAL COMPETITORS

Pigeons and doves were the avian species perhaps closest to *A. pertinax* in food habits. I observed chases (parakeet at dove, and vice versa), apparently related to food, among *A. pertinax* and Scaly-naped Pigeons (*Columba squamosa*), White-crowned Pigeons (*C. leucocephala*), Zenaida Doves (*Zenaida aurita*), and White-winged Doves (*Z. asiatica*). I found the parakeet had a moderately high feeding niche overlap (O_{jk},) with some species of columbids: notably O_{jk}(White-crowned Pigeon *versus Aratinga pertinax*) = 0.814, O_{jk}(Zenaida Dove *versus A. pertinax*) = 0.732.

Four common native bird species breed in cavities in eastern Puerto Rico. The Puerto Rican Screech-Owl (*Otus nudipes*) and Puerto Rican Woodpecker (*Melanerpes portoricensis*) were uncommon in the area (perhaps because of low nest cavity availability). The Pearly-eyed Thrasher and American Kestrel (*Falco sparverius*) were common at Roosevelt Roads and nested in cavities in hardwoods and palms. However, the kestrel preferred more open habitat (mixed palm-savannah) than the closed mangrove and canyon forests frequented by the parakeets. Pearly-eyed Thrashers were among the most common birds in the mangrove forest and were frequent nesters there. None of these cavity-nesting species used termitaria for breeding.

Both native psittacine species (endangered Puerto Rican Parrot *Amazona vittata* and extinct Puerto Rican Parakeet *Aratinga maugei*) are no longer in the lowland habitat in eastern Puerto Rico (Snyder *et al.* 1987). During the mid to late 1970s, 2 other exotic psittacines appeared in eastern Puerto Rico. Two Yellow-headed Parrots (*Amazona ochrocephala*) and one Rose-ringed Parakeet (*Psittacula krameri*) resided in the mangroves and uplands at Roosevelt Roads, but did not nest in the termitaria or tree cavities.

Exotic honeybees (*Apis melifera*) and roof rats (*Rattus rattus*) nested and roosted in tree cavities at Roosevelt Roads. Of the 9 tree cavities of adequate dimensions and condition within the 1.64 ha I sampled, 5 contained honeybee colonies and another a rat nest. Furthermore, of these cavities, only 5 were at a height suitable for nesting parrots, and of these, 3 were occupied by bees and rats.

ORIGIN OF THE ST. THOMAS POPULATION

Evidence presented here suggests that *Aratinga pertinax* could have, but probably did not, colonize St. Thomas, perhaps through a series of island hops originating in Curaçao. Although the distances among St. Thomas, Puerto Rico, and the intervening islands are not nearly so great as that between St. Thomas and Curaçao (ca. 770 km), my observations suggest that *A. pertinax* is capable of at least short over-water dispersal. Such movements may have been aided by tropical storms, which can be powerful agents of dispersal (Wiley, in press). One or more such dispersions, perhaps supplemented by subsequent events, could have landed sufficient birds on St. Thomas to establish a viable population.

However, *A. pertinax* does not commonly move over water to new islands, as evidenced by the fact that each of the Dutch West Indian islands with *A. pertinax* populations has a unique subspecies: Aruba — *A. p. arubensis*, Bonaire — *A. p. xanthogenius*, Curaçao — *A. p. pertinax*. Distances among these islands are not great: Aruba—Curaçao = 78 km, Curaçao—Bonaire = 52 km, Bonaire—Aruba = ca. 135 km. The distances between Venezuela and Aruba (30 km), Curaçao (70 km), and Bonaire (87 km) are also not great. These distances are about the same as those among the Virgin and Puerto Rican islands: Culebra Island to St. Thomas —25 km, Culebra Island to Vieques Island —15 km, Vieques Island to St. Thomas —35 km, eastern Puerto Rico to St. Thomas —60 km.

Perhaps a former effective barrier against the establishment of *A. pertinax* on other islands was the extensive *Aratinga* faunas on many of the Lesser Antilles (Fig. 3). Historically, endemic species of *Aratinga* occurred on Martinique, Guadeloupe, Dominica, and St. Lucia. Former competition with these native species may have been sufficient to prevent *A. pertinax* from establishing populations on these islands. No

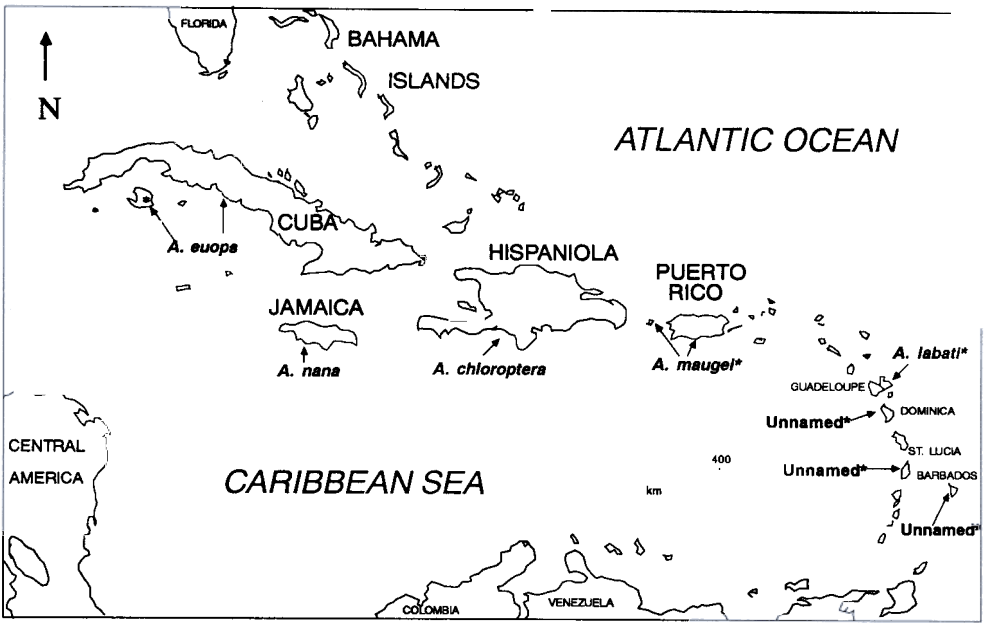

FIG. 3. Historic and present populations of native species of *Aratinga* in the West Indies. Extinct species and populations indicated by an asterisk.

native *Aratinga* has been reported from the Virgin Islands and Puerto Rico's endemic species, *Aratinga maugei*, is extinct.

The St. Thomas population of *A. pertinax* has been assumed by most authors to have originated through introductions from Curaçao stock (von Berlepsch *in* Hartert 1893, Hartert 1893, Nichols 1943, Marien & Koopman 1955, Forshaw 1989). Consistent with this hypothesis is that none of the islands between Curaçao and St. Thomas, including those closest to the Dutch island, has *A. pertinax* populations. Also, the historical and fossil records, though fragmentary, suggest *A. pertinax* was not present on these islands or the Virgin Islands in the past (Wetmore 1918).

Regardless of the means of dispersal, *A. pertinax* is likely a recent arrival in St. Thomas. The species seems quite plastic, and populations on other islands and the mainland show distinct racial differentiation. However, the St. Thomas population is considered identical with the Curaçao race (Hartert 1893). Although Marien & Koopman (1955) thought the St. Thomas population averaged smaller than the Curaçao race, it is likely that more extensive differentiation would have occurred in the time it took for the species to island hop to St. Thomas, and then disappear from intervening islands.

In summary, lack of records, differentiation, and intervening populations suggest that *A. pertinax* did not naturally spread to the Virgin Islands from a southern source population. The Brown-throated Parakeet was apparently a popular cage bird. It was harvested from Curaçao in large numbers (Hartert 1893) and was common in the pet trade in the West Indies and Europe (Russ 1895, Tavistock 1929, Seth-Smith 1903, Norton 1983). The popularity of the species as a cage bird and its regularity in the trade give plausible support for the hypothesis of introduction to St. Thomas.

RECENT EXPANSION TO PUERTO RICO

The range expansion reported here occurred at a time when the St. Thomas population had greatly increased in numbers since the hurricane-caused low numbers in the mid- to late-1920s.

Also, the parakeet had increased its range from primarily eastern St. Thomas to throughout the island. Recently, the species has been recorded from the adjacent islands of St. John and Tortola (Mirechi *et al.* 1977, Raffaele 1983).

The expansion of *A. pertinax* westward in 1975 was apparently not storm-aided. No severe storms occurred in this part of the West Indies in that year or in 1974 (National Climatic Center 1974, 1975).

Population characteristics of increase in numbers and range are favorable to natural range expansions. I believe the St. Thomas population, already expanding throughout that island and with small satellite populations appearing on St. John and Tortola, briefly expanded to Culebra, Vieques, and Puerto Rico through a series of island hops. Colonization was unsuccessful in all of these islands.

FACTORS INVOLVED IN THE EXTIRPATION OF THE EASTERN PUERTO RICO POPULATION

The probability of a colonizing population becoming established is higher when there is a large number of founders, a rapid rate of population increase, and minimum competition (MacArthur & Wilson 1967). The failure of *Aratinga pertinax* to colonize eastern Puerto Rico in the late 1970s may be the result of several interactive factors. The small size of the original innoculum with no further outside immigration into the population ensured a low probability of establishment. Competition with native and introduced animals may have also been a factor, but to an unknown degree. Although tree cavities for nesting evidently were limited in availability, termitaria of sufficient size for *A. pertinax* nests were abundant and, apparently, *A. pertinax* had no competition for these nest sites. Competition for food with other species is an unlikely reason for the parakeet's local extirpation. The food species used by parakeets and potential competitors (especially columbids) were plentiful in eastern Puerto Rico and available year-round through a succession of fruiting. Also, populations of potential competitors were depressed relative to historic times because of over-hunting and habitat degradation (Wiley & Wiley 1979, Wiley 1985). Furthermore, *A. pertinax* was able to feed on large fruits (e.g., mango) that were unsuitable for most other avian species, and extensively used exotic fruits abundant in natural and residential areas.

Predation is the probable major source of loss of the young and adult parakeets. Nest success and productivity were reasonably high, perhaps partly because bird nests in termitaria were protected from most forms of local predation by the incidental defenses of the host insects. However, mortality rates of free-flying birds were apparently high. Red-tailed Hawks (*Buteo jamaicensis*) are the most important predators of medium-sized birds, including parrots, in eastern Puerto Rico (Wiley & Wiley 1979, Snyder *et al.* 1987). When populations consist of few individuals and are confined to small areas, the stochastic loss of birds, even by low predation pressure, has substantial effect on population viability. Also, parrots, including *A. pertinax*, are flocking species, which derive survival benefits from the vigilance provided by the several individuals comprising the flock (Snyder *et al.* 1987, Westcott & Cockburn 1988). If numbers of individuals in a population are reduced to the level where insufficient birds are available for adequate predator vigilance, the risk of capture increases substantially.

An alternative explanation to the hypothesis of predator-caused extirpation of the parakeets at Roosevelt Roads may be that the birds dispersed to other, perhaps more favorable, sites. Although I failed to find *A. pertinax* populations in suitable habitat adjacent to the Roosevelt Roads study area, dispersed populations of *A. pertinax* have been reported from other parts of Puerto Rico since the observations recorded here. Nowhere has it become numerous (Raffaele 1983, Pérez-Rivera & Vélez 1980; Raul A. Pérez-Rivera, pers. comm.); the largest population is at Cabo San Juan, where small groups persist (about 8 birds/group; Pérez-Rivera, pers. comm.). The source of this and other populations in Puerto Rico have been suggested as escaped cage birds (Pérez-Rivera 1980).

IMPLICATIONS FOR CONSERVATION PROGRAMS

At the time of Columbus "discovery" of the West Indies, the region's parrot fauna consisted of no less than 28 species, including 7 macaws, 12 Amazon parrots, and 9 parakeets (Fig. 3). Less than 500 years later, that impressive array of uni-

que varieties has been reduced to only 10 species, including but 4 parakeets. Whereas all endemic species of *Aratinga* in the Lesser Antilles are extinct and most Greater Antillean species are declining or extinct, *A. pertinax* has expanded its range and increased its numbers on St. Thomas (Wiley 1991). These population changes are likely a result of improved protection from shooting and exploitation, extensive planting of exotic vegetation, which provides food and shelter for the parakeet, and reduced competition from native frugivores. Examples of other psittacine species, threatened or extinct in their native range, yet flourishing in their adopted homelands of suburban and urban environments, are common (Wiley *et al.* 1991).

Conservation programs for West Indian parakeets must incorporate strategies for managing the native species in the predominantly exotic, yet protected, suburban habitats — especially in this era of rapidly disappearing native habitats in the region. Conservation efforts must also address the threats posed by exotic psittacines. Introduced parrots may affect native species through competition for limited resources, by the spread of diseases, or through hybridization.

ACKNOWLEDGEMENTS

I thank Mary Hickman, Elizabeth Litovich, the late Hector O'Neil, and Beth Wiley for their help in observing parakeets. Herbert A. Raffaele and Cameron B. Kepler provided data on the parakeet from their unpublished field notes, for which I thank them. Raul A. Pérez-Rivera generously permitted me to use his observations on the current status of *A. pertinax* in Puerto Rico. I am grateful to Lloyd F. Kiff and Jim Jennings (Western Foundation of Vertebrate Zoology) and Eugene Cardiff (San Bernardino Museum of Natural History) for allowing me access to their egg collections. I thank Wylie C. Barrow, Jr., Gerald Lindsey, Oliver H. Pattee, and Marcia Wilson for suggestions which improved the manuscript.

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