

This species has been the subject of the most intensive conservation programme ever conducted on a parrot. Endemic to and probably originally present throughout Puerto Rico, it suffered from the almost total loss of its forest habitat and the crippling effects of being taken for pets and food, so that by the 1930s its population of c.2,000 was confined to rainforest in the Luquillo Mountains in the north-east of the island. Here it endured a long decline towards extinction that was only halted through major intervention beginning in 1968 and involving experiments with artificial nest-sites, controlling nest predators and competitors, and captive breeding. Recovery since the all-time population low of 13 birds in 1975 has been steady except for the impact of Hurricane Hugo in September 1989, and by the beginning of 1992 the population stood at a minimum 22-23 in the wild and 58 in captivity; after a record fledging success in July 1992, the wild population was 39-40.

DISTRIBUTION (All information in this section is derived from Snyder *et al.* 1987.) It is probable that the Puerto Rican Amazon originally occurred throughout Puerto Rico, since lack of distributional precision in early accounts may well have reflected its breadth of range, while in any case *Amazona* parrots are well known to wander widely from their most usual haunts. Certainly the evidence reveals its former presence in all major vegetation types on the island except the dry forests of the southern coastal strip, although even there it is probable that the bird occurred (see Remarks 1). The current range in the Luquillo Mountains, covering some 1,600 ha, represents a mere 0.2% of its former area of distribution (see Remarks 2).

A subspecifically distinct population, *gracilipes*, formerly occurred on Culebra off the east coast (it was common there in 1899 but had disappeared by 1912), bones of the species have been found on Mona, and reports of parrots, presumably of this species, are known from Vieques and St Thomas (the latter in the U.S. Virgin Islands).

POPULATION (Unless otherwise stated, all information in this section is derived from Snyder *et al.* 1987.) Early evidence is that the species was originally abundant on the island, and indeed extrapolation from 1956 figures yields a conservative figure of 84,000 birds for pre-Columbus times, the true number being perhaps several hundred thousand or even a million. Although in the second half of the last century the species was still considered abundant in many areas, it was evidently in steep decline throughout the period, which witnessed the most drastic reduction in forest cover in the island's history (see Threats).

In the twentieth century the species survived in the Guajataca area until about 1918-1920; at Río Abajo until 1925, and not beyond 1928; in the Sierra de Cayey until at least 1936; and in the areas adjacent to the Luquillo Mountains down to around 1960, after which all records are confined to the forest on the mountains themselves (although parrots have sometimes been observed leaving Luquillo's western flanks on long flights, especially during summer). In 1937, when the species was apparently confined to the north-east of the island centred on Luquillo Forest, an estimate of 2,000 birds was made, although the director of the Forest Service in the 1920s felt this to be far lower than the number of birds present during his tenure of office (the decline, if real, might have been attributable to the impact of the 1928 and 1932 hurricanes: see Threats). By the 1950s the population had dropped to around 200, although the error factor in the censuses then may have been $\pm 25\%$. Then in May 1963 a minimum 130 and possibly over 200 were observed. In December 1966 70 were counted in a single flock, probably with an accuracy of ± 10 , although there is no evidence that this represented the entire population at the time. However, less than two years later, in November 1968, at the start of the second major study of the species, only 24 birds could be found. Over the next three years the population continued to decline, and in February 1972 two birds were trapped from the wild population of 16; although there was some recruitment in the following three years, other losses led to the population being a firm minimum of 14 at the start of the 1975 breeding season, briefly dipping to 13 with the death of a nesting adult, this figure representing the lowest the species has ever reached in the wild. With six young fledging that year, and with further slight gains in recruitment against mortality, the wild population rose to 25-26 in 1979. In 1980 only 18 birds survived but fledged eight young (including two fostered from captivity), making 26; in 1981 the equivalent figures were 19, 10 (1), 29; in 1982 numbers at the start of the breeding season were unknown, 8 (3), 26; in 1983,

25-27, 6 (3), 31; in 1984 29, 4, 28; in 1985 25, 12, 37; (information hereafter from F. J. Vilella *in litt.* 1992) in 1986 28, 4, 28; in 1987 33, 8, 36; in 1988 36, 4 (2) 30; in 1989, 30, 7 (2) giving a total of 47 in September when Hurricane Hugo struck; in 1990 21, 2, 23; in 1991 23, 7, 30, with six pairs breeding in the wild (the highest since the 1950s: Wilson *et al.* *in press*); in 1992 21-23 birds were known to be alive before the breeding season (and by early July all 11 chicks, 10 of them wild-born, had fledged, a record for the project, bringing the total wild population to 39-40 birds), but in this case as in that of the low post-breeding total in 1988 and pre-breeding total in 1989 (both 30) the counts may have been influenced negatively by adverse weather.

The development in numbers of the captive flock from two in 1970 to 29 in 1986 and 58 in 1992 is given in Measures Taken: Captive breeding.

ECOLOGY (Unless otherwise indicated, all information in this section is derived from Snyder *et al.* 1987; but see also Rodríguez-Vidal 1962.)

Original parrot habitats In its original state Puerto Rico supported eight major climax vegetation types, all of them forest and in combination extending from the shoreline to the highest peaks of the (predominantly mountainous) island. Of these types, moist coastal forest covered 27% of the island in the north, east and west, moist limestone forest covered 17% in the north and north-west, dry coastal and dry limestone forest covered 13% and 2% in the south, lower Cordillera and lower Luquillo forest covered 32% and 1.5% in the centre, and upper Cordillera and upper Luquillo forest covered 6% and 1%, also in the centre, with 0.5% given over to mangrove and littoral scrub forest; records exist of the Puerto Rican Amazon's occurrence in all but the two dry forest types, although it is believed that it occurred there nevertheless (see Remarks 1), while its presence in mangrove and littoral scrub forest is judged to have been largely seasonal, although some birds may have been resident.

Current parrot habitats The area in which the species now remains is upper Luquillo tropical rainforest, between 200 (150 since 1990: J. M. Meyers *in litt.* 1992) and 600 m, wetter than elsewhere on Puerto Rico and considered a distinct ecological province of the island. Four broad forest types exist in Luquillo in response to soil, rainfall and wind: (1) tabonuco forest, a classic diverse tall rainforest formation, occurs on lower mountain slopes (covering 5,430 ha within the national forest, although only a few hectares are old-growth) and is dominated by tabonuco *Dacryodes excelsa*, which before the largest specimens were logged was extremely important as a source of both food and nest-sites for the parrot; immediately above this lies (2) the palo colorado zone (covering about 3,400 ha), a depauperate upland swamp of short-statured trees, is characterized by palo colorado *Cyrilla racemiflora*, whose susceptibility to heart-rot makes it an important source of nest-sites and hence now the chief zone in which the parrot occurs; (3) sierra palm *Prestoea montana* forest (covering 2,050 ha) forms dense, virtually monocultural patches on highly eroded soils within the altitudinal range of the two previous types, and provides fruit in enormous abundance such that parrot breeding is timed to coincide with fruiting and parrot movements during much of the year are explicable in terms of palm fruit availability; and (4) dwarf forest (covering 450 ha) is the upper limit formation and of no significance to parrots except for occasional perches, although F. J. Vilella (*in litt.* 1992) reported several important food sources – e.g. *Clusia* and *Miconia* – and sufficient frequency of parrot occurrence in this habitat that it must serve the species on occasion for foraging. Analysis of habitats used by breeding and non-breeding parrots in 1991, two years after Hurricane Hugo, detected no significant differences, although such differences did exist between nesting areas themselves (Meyers and Barrow 1992).

Food and feeding Birds feed primarily on fruits, procured with the bill, normally one at a time in a slow deliberate manner, although in quite large amounts in relatively short periods: with spatially concentrated foods such as sierra palm, birds can fill their crops in well under an hour, and in the case of the sierra palm about 130 fruits constitute one meal. The species has been recorded feeding on at least 60 plant species in Luquillo (see Appendix 8 in Snyder *et al.* 1987), with most records being of fruits, seeds or leaves of trees (44 species), shrubs (seven species) and vines (seven species). Birds rarely descend near the ground but have been seen feeding about 2 m up on *Miconia* fruits and *Psychotria* bark; sierra palm accounts for 22% of the records, and the next most frequently observed food, tabonuco, accounts for less than 7% of the total, indicating the catholicity of usage in the species; only 62% of feeding observations

come from the top ten species. Non-fruit items (chiefly leaves) are eaten frequently enough to be significant if minor components of the diet, and are associated with the breeding season, possibly because they contain specific nutrients important for reproduction. Flowers of *Piptocarpa tetrantha* and bracts of *Marcgravia sintenisii* are consumed for their nectar. On a species total basis, there may be some avoidance of small fruits, possibly through time/energy and/or predation-risk factors. Although fruiting in many trees is almost year-round, those most favoured by the parrots show pronounced peaks, thus causing variation in use of forest zones by parrots. Sierra palm bears fruit throughout the year, but maximum seed drop (indicating maximum crop of edible fruits) occurs between February and April, and parrots feed heavily on the species from January to May. Towards the end of the breeding season and into summer the species exploits cupeillo *Clusia grisebachiana*, and when this declines they switch largely to tabonuco through the fall and winter. Since the maximum flight time between extremes of the present range within Luquillo is only 10 minutes, much flight activity may provide birds with information on the state of various foods. The species certainly once descended to crops, as it was recorded in 1836 that great flocks destroyed whole fields of corn, and this habit might have led to its extermination on Culebra (but see Threats for alternative explanations). During incubation, females are virtually confined to their nests and their mates provide them with almost all their food, on average 5.4 times a day.

Nest-sites The species breeds in natural cavities in trees produced almost wholly by decay, although it formerly used potholes in limestone cliffs in Río Abajo. Analysis of records indicates that birds are very conservative in their choice of nesting areas in Luquillo, almost all records in the 50 years to 1980 being from five areas, North Fork and South Fork in the west, and East Fork, West Fork and Center Fork in the east, although since Hurricane Hugo two new nesting areas (involving a pair each, with all four birds born since 1986) have been found or have become established, on East Mountain, c.1 km from the East Fork area, and Quebrada Grande, in the next valley south from South Fork (F. J. Vilella *in litt.* 1992).

Of 25 nest trees documented in 1945-1986 all but one were in palo colorado, the exception being a laurel sabino *Magnolia splendens*, although older evidence exists that the species has used tabonuco and caimitillo *Micropholis* spp.; elsewhere in Puerto Rico nests have been reported from corcho *Pisonia subcordata*, aguacate *Persea americana*, jácana *Pouteria multiflora* and royal palm *Roystonea borinquena*.

In 1991 at the new site in East Mountain the first confirmed use of tabonuco was recorded, the cavity in question being more similar in structure to cavities found in trees of coastal forest currently used by exotics (F. J. Vilella *in litt.* 1992; see Remarks 1). An important factor in re-use of nests is cavity durability; the longest-lasting tree nest cavity recorded survived for 20 years, the average being between 10 and 15 years; qualitative evidence suggests that females select nest-sites. Nest-sites can be very close, once 33 m, once 15.2 m, once 4 m, though this is not usual; however, nests appear to be clumped within the forest, location of parrot nesting areas appears to have no strong relationship with good feeding areas, and the overall breeding distribution appears to reflect cavity availability. Birds seem to prefer deep or possibly dark sites; they also prefer the largest cavities available. Wetness, coupled with deepness, most severely governs the availability of nest-sites. Optimal sites are at least 4.5 m from the ground, and are dry, flat-bottomed, at least 60 cm deep, dark within, with entrance widths of at least 6 cm and internal diameters of at least 23 cm at the bottom; minimal sites may be any height from the ground, as shallow as 25 cm, with internal diameters at least 15 cm; the former are rare, the latter relatively common.

Breeding success and related behaviour In most recent years a substantial fraction of pairs in the population have defended territories in the breeding season, but a substantial fraction of these pairs (nearly half) have failed to lay eggs, a major factor militating against recovery of numbers; from 1976 through to the mid-1980s the number of actual breeding pairs in the wild population remained virtually constant at four, despite a gradually increasing total population, and only when the population reached about 40 individuals in 1989 did new breeding pairs begin to appear (N. F. R. Snyder *in litt.* 1992).

In the past, failure to breed may have reflected failure to find suitable nest-sites, but may also be explained in terms of immaturity and inadequate compatibility or other factors. Territorialism can be vigorous but is related primarily to nest defence, with pairs sometimes driving out intruders as far as 140 m from the nest; the frequent abandonment of the nest hole for territorial defence is a major liability in relation to nest-predation by Pearly-eyed Thrashers; moreover, birds take little notice of their surroundings during defence, and probably then are especially vulnerable to predation by hawks. Territories are

defended year-round to some extent, but much more vigorously in the breeding season. Because of the apparent abundance of limestone holes at Río Abajo, there seems to have been no strong territorialism in the population there. In almost every observed instance newly territorial pairs have established themselves immediately adjacent to territories of breeding pairs, a tendency that helps explain the extreme stability of nesting areas. Parrot pairs nevertheless check other sites continually, probably as a type of insurance. Timing of breeding coincides with maximum production of sierra palm, but may also be linked to the “dry” season, important because dry cavities are essential to reproductive success. Calculated dates of first eggs are between 11 February and mid-April (most late February to early March), with all evidence pointing to incubation starting with the first egg; on average the hatching interval between eggs is two days, following a 26-day incubation period; although the egg-laying period coincides with the driest time of the year, in lowland Puerto Rico egg-laying occurred considerably earlier and it would seem that other factors, such as fruiting of major foods, are the chief trigger of breeding. Clutch-size varies from two to four, mostly (and mean) three; reports of up to six may have involved two females. Eggs are incubated exclusively by females. All 67 eggs laid in the wild and not predated, 1973-1979, were fertile, 56 hatched, and only one gave rise to an abnormal chick. Adults feed their young on demand, though as the latter grow, their crops expand greatly and feeding frequency declines accordingly; when close to fledging, young actually become reluctant to take food, perhaps in order to make the first flight (which is seemingly haphazard and sometimes disastrous) more buoyant. Length of nestling stage averages about nine weeks, but varies considerably, the fledging date showing an inverse correlation with egg weight. The female stays with the chicks throughout the first week and a half after hatching, but then undertakes morning and sometimes evening foraging trips with her mate; she roosts with the chicks right through to fledging; however, in one case a widowed female fed and reared chicks essentially unaided by a new partner. Adults are extremely circumspect in approaching fledged young, suggesting high risk of predation, and it may be that large broods present difficulties of management through the dependency stage, resulting perhaps in greater risks of mortality to the adults as well as to their offspring. Families stay together after fledging, certainly (in one case) for five weeks and almost certainly (from fragmentary observations) into the fall, tending to disband in winter. A radio-telemetry study of juvenile parrots showed that they stayed 58 ± 29 days in the natal valley (except in one case where the killing by a raptor of one of a brood of two led to the immediate movement by the surviving family to an adjacent valley), ranging over up to 32 ± 10 ha in one year though only 13 ± 6 ha in another, later integrating with adult flocks 33-95 days after fledging, when they then ranged over much larger areas (1,243 ha in 1986 and 822 ha in 1987) (Lindsey *et al.* 1991; see also Lindsey and Arendt 1991). However, first-year birds appear around the natal nest-sites in the early stages of the next breeding season, only to be chased off silently by their parents, and this behaviour is helpful in calculating first-year mortality rates in the species, put in the 1970s at 32.5%. Post-juvenile subadult mortality then appeared to be around 15.2%; and adult mortality was around 9%; however, in the early 1980s while adult mortality was only 6.8%, post-juvenile subadult mortality rose to 29%, for unknown reasons (this was the stimulus for the radio-telemetry study of the mid-1980s, which showed that predation by Red-tailed Hawks *Buteo jamaicensis* was significant: Lindsey *et al.* 1988). In the 1970s nest success increased from a historically low rate of 11-26% to around 69% for pairs laying eggs, i.e. 1.5 young fledged into the wild per egg-laying pair, but only because of a wide variety of measures; this was maintained in the period 1980-1985. Evidence from the wild and captivity suggests that age of first breeding may generally be four.

Social organization (spatial and temporal) The basic social unit is the pair: of 413 sightings of flying parrots in the non-breeding season, 1968-1969, 307 (74%) were of two birds, 73 (18%) of singles, 23 (6%) of trios and 10 (2%) of anything larger; trios were usually a pair plus an extra bird, commonly a juvenile offspring. Members of mated pairs stay close together (less than 2 m when flying) throughout the year, except in the weeks when the female is egg-laying, incubating and tending small young; but pairs do not automatically represent mated pairs, as juveniles of single broods tend to stick together through their first year, even when not with their parents. Pairs usually remain constant over the years; however, when one member of a pair is lost, re-pairing can be rapid, with one case of a male abandoning his injured mate for a healthy, recently widowed female. Most feeding observations (79%) have fallen between 06h00 and 09h00 and between 16h00 and 19h00; 41% between 07h00 and 08h00 and between 17h00 and 18h00,

indicating peak foraging times. Birds feed during the morning (they stop calling at 09h30), then retire to roosting trees where they stay over midday, rarely becoming vocal until c.16h00 (some feeding may of course occur over midday). An increase in the number and intensity of calls and flights after 15h30 heralds the afternoon feeding period. Birds have never been observed returning to their roosts after dark, and it is highly unlikely that they ever fly at night. Feeding is relatively gregarious: of 92 feeding observations, 1968-1976, 11 (12%) were solitary, 43 (47%) were in pairs, and 38 (41%) were in groups of three or more; anti-predator sentinels appoint themselves at feeding flocks. Birds do not roost in holes during the non-breeding season, and when breeding the female does so, in the nest cavity. Birds roost in the nesting areas for much of the year, and by the middle of the breeding season assemble there each night, which is when census work can be considered most reliable. Parrots generally leave their roosts an hour after sunrise and return about an hour before dark.

THREATS (Unless otherwise indicated, all information in this section is derived from Snyder *et al.* 1987.) Among important threats to evaluate have been a diversity of man-caused problems, including cutting of the original forests, hunting, harassment in agricultural lands, pet-taking, and the steady selective loss of potential nest holes resulting from (a) competition from introduced honeybees *Apis mellifera* and (b) felling of trees in which bees nest. Among natural threats have been nest predation and competition from Pearly-eyed Thrashers *Margarops fuscatus*, parasitism by warble flies *Philornis pici*, and predation by Red-tailed Hawks. There is now a firm belief that as soon as one problem is brought under control another arises to take its place: complexity and unpredictability are central to the problems faced by the species.

Habitat loss Although European settlement of Puerto Rico was initially slow, with only 880 Spaniards by 1650, the human population was 45,000 by 1770, 100,000 by 1790, 500,000 by 1850 and 1,000,000 by 1900, and it was during the second half of the nineteenth century that the major destruction of habitat occurred, so that by 1912 less than 1% of the island's original forests were virgin. Even Luquillo Forest was reduced to 2,270 ha of virgin habitat by the turn of the century. A timber stand improvement scheme in Luquillo, begun in 1945, led to the selective removal of palo colorado from at least 1,620 ha of prime palo colorado forest, and this may have been highly damaging given the species's dependence on this tree for nest-sites. Moreover, selective felling of trees with cavities, to obtain either nestlings or much more frequently honey, will have had the long-term effect of critically reducing the number of available nest-sites for parrots. There is a recurring proposal to reopen the 191 road through the Luquillo Forest, which it is believed (despite Fish and Wildlife Service findings) would jeopardize the prospects of the parrot recolonizing (predicted to happen soon) the formerly important Icosos valley (J. W. Wiley *in litt.* 1992). The U.S. Forest Service has attempted to increase timber cutting within Luquillo and, although this has been rejected, the issue may be revived (J. W. Wiley *in litt.* 1992).

Hunting Parrots were hunted in the mangroves at Mameyes Swamp only 16 km from Luquillo in 1912, the last lowland locality at which the species was recorded. The race *gracilipes* was exterminated by settlers on Culebra apparently in retaliation for its feeding on crops, although Phillips (1929) considered its loss to have been contributed to by the establishment of a naval base there, and there is good evidence that a hurricane was to blame (see below). Hunting was not, however, significant in the Luquillo region until the mid-1960s, when it apparently became "especially common"; the severe downturn in parrot numbers in the late 1960s may therefore possibly be attributable to this abuse.

Pet-taking Relentless hunting and pet-taking in combination may have caused the final extinction of local populations in many areas, e.g. around Guajataca and at Río Abajo. Pet-taking is implicated in the final extinction of the species in the Sierra de Cayey. Pet-taking was rampant in certain areas around Luquillo during this century until the 1950s, e.g. in the Fajardo valley, Icosos valley and notably on the western side of the mountains, where in 1948 10 trappers each took 6-12 parrots per year, a harvest that may have represented the entire annual reproductive output of the species in the region. Nest-robbing continued in Luquillo into the 1960s at the North Fork nest.

Translocation attempts A large number of nestlings were removed from the population in the mid-1950s in an attempt to reintroduce the species into several other forests; many dozens of chicks were taken in each of the two years of this experiment (1956 and 1957 or 1957 and 1958). Healthy fledglings

were released in groups in several forested sites in central and western Puerto Rico including Toro Negro, Maricao and perhaps Guajataca forests, but none is known to have survived. A strong negative impact on the Luquillo population can be assumed.

Radiation and other factors in the late 1960s From January to April 1965 part of Luquillo was deliberately exposed to high-intensity radiation to determine the response of rainforest vegetation. Although no evidence of direct parrot mortality was found, some may have occurred; and although it is not clear how this could explain the precipitous fall in numbers after December 1966 (observations in 1969 indicated that only two pairs were nesting), it cannot be ruled out as a contributory factor. Warfare manoeuvres were undertaken in Luquillo, 1966-1971, but seem unlikely to have been a serious influence. Herbicide experiments in 1967 took place outside the normal range of the parrot and were probably insignificant; construction of the East Peak Road in the late 1960s may have caused disturbance to a parrot area, but seems unlikely to have caused any mortality; and microwave emissions from the East Peak radar station since 1965 has had an unknown impact on parrots.

Hurricanes and drought The population at Río Abajo was considered not to have recovered from the impact of San Ciriaco in 1899, and any remnant population (which had then suffered from trapping and shooting and further logging) would have been annihilated by the great 1928 hurricane San Felipe that directly hit the area. San Ciriaco might well have been responsible for exterminating the last representatives of the Culebra race *gracilipes*, given that the bird was present on the island in February 1899, the storm struck in August, and the following year no birds were seen (Pérez-Rivera and Bonilla 1982). San Ciriaco and San Felipe also devastated the Sierra de Cayey, allowing for rapid opportunistic human settlement. San Felipe, regarded as the worst storm to have struck the island, was followed only four years later by San Ciprián (1932), and both these had major impacts on the Luquillo Mountains, causing direct death to parrots, indirect losses from subsequent starvation and, possibly, reproductive depression through removal of nest-trees (although one effect of hurricanes is to cause a pulse in fruiting, this possibly being the cause of the enhanced reproduction of parrots observed in the years after Hugo, notably in 1991: N. F. R. Snyder *in litt.* 1992). A major drought in 1967 coincided with the period of maximum rate of decline in the Puerto Rican Amazon, but although birds may have been stressed by this it seems unlikely to have been the primary cause of mortality.

On 18 September 1989 Hurricane Hugo tracked directly across Luquillo, with maximum sustained winds of 225 kph: of the 45-47 parrots counted in August, only 21-23 could be found at the end of September, and their behaviour had radically changed, with birds very quiet and in small groups instead of the flocks usually encountered at that time of year (M. H. Wilson *in litt.* 1992). The loss of 50% of the population was probably mostly attributable to the virtual loss of food and cover in Luquillo for 2-3 months afterwards, during which time parrots were observed almost daily leaving the forest in the early morning presumably in search of food and returning in late evening to roost (F. J. Vilella *in litt.* 1992). All five nest trees survived the onslaught, and although breeding in the following year was late, in March three pairs laid a total of eight eggs, all fertile, five hatching and two young fledging (M. H. Wilson *in litt.* 1992).

Bees Introduced honeybees *Apis mellifera* are now common in Luquillo, usually nesting in palo colorado cavities. It is not known if they can evict parrots from nests, but their occupancy of many good potential sites probably reduces nest-site availability for the parrots; in the period 1973-1979 five parrot nests were taken over in the post-breeding period by bees (see Measures Taken: Bees).

Warble-flies Warble-flies or bot-flies *Philornis pici* parasitize birds of several species in Luquillo at relatively high levels, e.g. 11 (25%) of 44 young Puerto Rican Amazons, 1973-1979; of these, four would have died without intervention. Warble-flies may have increased in Luquillo in response to an increase there of their most favoured host, the Pearly-eyed Thrasher. In 1984 a chick was lost to soldier-fly *Hermetia illucens* larvae, not previously noted to behave in a predatory manner.

Non-avian vertebrates The Puerto Rican Boa *Epicrates inornatus* was reported once to have been seen about to enter a nest and it seems highly likely that it is an occasional predator of eggs and young. There is an ever-present risk of monkeys becoming established in the forest, and there are already reports of rhesus monkeys *Macaca mulatta* colonizing the island (there is in fact a feral colony of these monkeys in the Sierra Bermeja, although this is 140 km from Luquillo: R. A. Pérez-Rivera *in litt.* 1992). Cats *Felis*

catus are common in Luquillo, but there is only one recorded case of cat predation on parrots, dating from the 1950s, and the threat is not thought significant. The roof rat *Rattus rattus* is common in Luquillo, and was believed in the 1950s to be the single most important threat to the parrot, with four apparent cases of predation of nests out of 16 studied; while reanalysis of these cases in the light of subsequent experience suggests that the rats may have been scavenging in nests deserted or lost for other reasons (Snyder *et al.* 1987), it is still felt that the risk is significant and the rat control programme is important to continue (R. A. Pérez-Rivera *in litt.* 1992). Since 1956 (see Measures Taken: Rats) there have been no clear cases of loss of nests to rats.

Raptors There is no evidence that either of the two threatened endemic raptor subspecies (see Remarks) poses a serious threat to the Puerto Rican Amazon, but two other raptors, the Red-tailed Hawk and Peregrine *Falco peregrinus* give cause for concern. The Red-tailed Hawk is the most abundant raptor in Luquillo and the most important predator faced by the parrot: attacks have been witnessed, a dead female was almost certainly victim of the species, two of three radio-tagged fledglings released in 1985 were apparently killed by the species, and three cases of (attempted) nest-predation have been recorded, the last of which was terminated by an observer from a hide; possibly as many as nine of the nest failures recorded since the 1950s were caused by this species (more recent work has confirmed this species as a particular threat: Lindsey *et al.* 1988). The Peregrine is not regular in winter in Luquillo, but a male once took up residence for three months; if such a bird ever keyed in on parrot foraging flights the population could be rapidly decimated, and in the absence of a solid explanation it is at least possible that the population crash of the late 1960s was caused by such a development.

Pearly-eyed Thrashers These are the most remarkable natural enemy of the parrot, particularly common in the palo colorado zone of Luquillo; they probably do not enter parrot nests in order to prey on the contents (no ingestion of victims has been seen), but quickly attack if they find eggs or young in occupation. In the 1950s only one of the 10 cases of nest failure documented was attributable to thrasher attack, but this reflects much lower density of thrashers then; a five-fold increase in their numbers occurred in the 20 years to 1976, probably in the decade to 1963, and since 1968 at least five nest failures have been attributable to the species; factors limiting thrashers include nest-site availability and warble-fly parasitism. The species may only have arrived on Puerto Rico in the mid-nineteenth century (no subfossil bone deposits are known, despite its habit of nesting in cave entrances), and it was certainly rare there at the end of the century; hence perhaps the parrot's poorly developed defences to the species.

Accidents, injury and disease One cause of nest failure has been tree fall (two cases since 1954) and another is death of young by drowning in the cavity (one case in the 1950s). Recent studies have shown that birds can injure themselves accidentally if panicked or when flying at low light intensities, and damage each other deliberately during disputes over nest-site ownership. Meanwhile, large numbers of exotic psittacines have been imported into Puerto Rico in recent decades, and although no species has yet established itself in Luquillo some have been seen on the fringes (and there have been two sightings inside the forest since 1990: J. M. Meyers *in litt.* 1992); the diseases they may be carrying could easily be transmitted to the endemic (and presumably less resistant) species, and in the absence of a solid explanation it is at least possible that the population crash of the late 1960s was caused by such a development.

Poor breeding performance For reasons that can only be speculated on, the failure of the population in the late 1970s and early 1980s to form more new breeding pairs was discouraging. Moreover, few pairs were then laying eggs and several pairs only fledged young because of fostering captive-bred offspring into their nests. While the pairs laying eggs continued to exhibit good nesting success (69%) through this period (under intensive management), nearly half of all territorial pairs remained non-breeders. The exact causes of failure to lay eggs have remained difficult to document, but in the most recent years have apparently not been a function of nest-site availability, as many suitable nest-sites have been provided in the nesting areas; the upswing in reproductive effort associated with (a) the population reaching a size of about 40 individuals in the late 1980s and (b) the massive fruiting of forest trees post-Hugo suggests the existence of some density-dependent controlling factors and the possible importance of nutritional and perhaps other factors (N. F. R. Snyder *in litt.* 1992). One such factor might be inbreeding depression: DNA fingerprints of successfully captive breeding pairs of Hispaniolan and

Puerto Rican Amazons had average bandsharing coefficients of 0.29 and 0.34 respectively, while those of unsuccessful Puerto Rican Amazons had a significantly higher average of 0.47, which suggests that unrelated Puerto Rican Amazons are inbred and that inbreeding depression is partly responsible for the low number of successfully breeding pairs (Brock 1991).

MEASURES TAKEN (Unless otherwise stated, all information in this section is derived from Snyder *et al.* 1987.) Habitat conservation in Luquillo on behalf of the Puerto Rican Amazon was recommended in separate reports in the late 1940s, and for the most part the lands identified have been maintained free of significant development by the Forest Service, although in the 1950s it rapidly became clear that habitat conservation was insufficient to guarantee the preservation of the species. The first study of the Puerto Rican Amazon itself was carried out in 1953-1956 by the Commonwealth of Puerto Rico government supported by the Pittman-Robertson Program of the U.S. Fish and Wildlife Service (see Rodríguez Vidal 1962). The second study began in 1968, following the placing of the species on the Endangered Species List in 1967, as a cooperative programme of the U.S. Fish and Wildlife Service, U.S. Forest Service and the Commonwealth of Puerto Rico government (through its Department of Natural Resources), with important support from WWF, and continues today. This has involved over 20,000 hours of observation (making it possible to identify and evaluate some of the major stresses on the species) and years of thought and analysis, yet a full understanding of the causes of the species's endangerment remains to be achieved; the validity of scientific generalization is greatly compromised by sample size, and with a tiny population dwindling towards extinction the critical factor has been time, so that measures have had to be implemented rapidly "on the basis of incomplete information, intuition and hope".

Hunting Since 1974 increased patrolling of the forest has led to a decline in the frequency of gunshots heard in Luquillo.

Rats In 1956 and 1957 rat control (poisoning and metal guards on nest trees) was practised, and it was reinstated at the start of the second study in 1968 and continues down to the present.

Bees The five honeybee colonies established in parrot nests after breeding in the period 1973-1979 were simply exterminated. Now the preferred method for ensuring that nest-sites remain available to parrots is to close them off after fledging in June until the end of the swarming season in September.

Pearly-eyed Thrashers Between 1973 and 1976 attempts (successful) were made to guard all parrot nests from thrashers through direct observation and the use of pellet guns (a minimum of 26 thrashers were shot at one nest-site in 1973), while from 1975 experiments were made with the substitution of plaster eggs over the incubation period so as to allow concentration of efforts on other nests. A nest-site design attractive to parrots but not to thrashers was developed and deployed, and the provision of alternative sites for thrashers nearby has resulted in resident pairs of the latter greatly reducing visits from prospecting conspecifics; these two factors in combination appear to have resolved the problem (but the continuing nest-watch programme is important in monitoring the situation in case of complications: J. W. Wiley *in litt.* 1992).

Warble-flies The only effective counter to infestation of chicks is to check them regularly and remove and treat any that are affected, and at least three birds have been saved from certain death in this way. A remarkable drop-off in infestation since 1979, despite no observed decline in warble-fly populations in the forest, may be the result of the deeper, darker nest-cavities made to foil thrashers.

Nest-site increase and enhancement In the belief that very low nest-site availability might be inhibiting birds from breeding, many nest-boxes were installed in the forest in 1969 and 1970, although these were not used, probably because too small. Further nest-boxes were installed over the coming years; from 1973 natural nest-sites were improved by creating artificial substrates or greater space, and since 1975/1976 all breeding pairs have been using sites either created or rehabilitated by man. All parrot nests have been modified to prevent entry by Red-tailed Hawks. In 1989 Hurricane Hugo destroyed most nest-boxes in Luquillo, and the Forest Service elected not to replace them but to focus efforts instead on enhancing natural cavities in living palo colorado trees, scooping existing holes to a greater depth, drilling drainage channels, using chicken wire as a false bottom, and/or attaching a sheet zinc visor to the entrance, all to ensure dry nesting; by mid-1992 47 cavities had been enhanced by the Forest Service in parrot nesting areas, and three of them were adopted by breeding pairs in 1991 and 1992, one of these being in a

valley previously not known to be occupied by nesting pairs (E. R. García *in litt.* 1992; also Meyers *et al.* in prep.).

Direct assistance In a case where a chick was so affected by slime inside the cavity that it could not fledge, moulted feathers from a captive bird were “imped” onto its wings and tail to allow it to do so. Interventions from hides have prevented predation of nests by Red-tailed Hawks and Pearly-eyed Thrashers. As many as six nests that were successful between 1973 and 1976 might have been lost to thrashers without intervention. Increased vigilance since 1987 has resulted in further successful interventions (Lindsey *et al.* 1989).

Monkeys A small colony of monkeys *Saimiri sciureus* released into Luquillo Forest by an unknown agent was removed just in time in 1973.

Captive breeding A captive breeding programme for the species was begun in 1970, as a safeguard against extinction, a source of biological information unobtainable from wild birds, and a reserve from which the wild population could be supplemented either in Luquillo or in due course elsewhere. An aviary was established in Luquillo itself in 1973. The original stock consisted of two old zoo birds donated in 1970, two wild birds trapped in 1972 and five young taken as eggs or chicks in 1973; since then the emphasis has fallen on adding representatives of different genetic stock, and as of 1979 every pair that had bred in the wild since 1972 had descendants in captivity. In 1979, when the stock stood at 15 birds, nine females and six males, the first captive breeding occurred and the offspring was fostered into a wild nest where it fledged successfully. In the period 1979-1986, although only four wild birds were added to the stock, it increased to 29, 10 females, seven males and 12 unsexed juveniles.

In 1986-1988 another nine birds were added to the wild stock, but the captive population continued to increase to 47 birds (of which 16 were known to be female, 20 male); the captive flock was unaffected by Hurricane Hugo, with no birds lost and as many eggs laid and young fledged in 1990 as in 1989 (M. H. Wilson *in litt.* 1992), and before the start of the 1992 breeding season the total stood at 58 birds (F. J. Vilella *in litt.* 1992). As in the wild, the number of breeding pairs in the captive flock remained low, around four (Wilson *et al.* in press). Studies of the birds' nutritional requirements and genetic diversity have therefore been undertaken, along with research on artificial insemination techniques and artificial incubation (Lindsey *et al.* 1989). A second captive facility at Río Abajo, constructed with reintroduction there in mind (see Measures Proposed: Reintroduction), is not yet finished, but 12 birds may be moved there by the end of 1992 or at the start of 1993 (J. M. Meyers *in litt.* 1992).

Other developments since the mid-1980s Wild nestlings have been sexed and fitted with steel leg bands; a volunteer nest-watch programme since 1987 has increased coverage of nests substantially; survival, movement and behaviour of parrot young has been studied using radio-telemetry; in 1988 a study of the distribution and territorial behaviour of non-breeding parrots was initiated; and release strategies have been developed for optimizing the survival of captive-raised birds when returned to the wild (Lindsey *et al.* 1989). Studies have also been conducted on the reproductive behaviour of the species, on its territorial behaviour, on its vocalizations, on constant character differences in vocalizations between pairs, and on capture and marking of surrogate psittacines (M. H. Wilson *in litt.* 1992). The Forest Service has built (or, after Hugo, rebuilt) 34 look-out towers for monitoring operations (E. R. García *in litt.* 1992).

A population viability analysis was conducted on the Puerto Rican Amazon in June 1989 under the auspices of CBSG (Lacy *et al.* 1989); although its recommendations for a metapopulation (i.e. several as far as possible self-sustaining subpopulations) were felt inappropriate or at least premature (see Measures Proposed) it has had the effect of intensifying the build-up of the captive population, and this appears in part to have been at the expense of the programme to release captive-bred birds into the wild population, discontinued since 1986 (J. W. Wiley *in litt.* 1992). DNA “fingerprinting” has allowed the development of a genealogy (by K. M. Brock) and hence the planned maximization of available genetic variation; captive pairs are being allowed to rear their own young, aiming at future releases of captive-bred birds (F. J. Vilella *in litt.* 1992).

Following Hurricane Hugo in September 1989 a number of new management techniques have been introduced. New observation blinds have been built at newly active nests; steel leg bands have been coloured through electroplating, and parrot chicks are now individually marked using band combinations; and census methods have been modified to increase precision and sample size (F. J. Vilella *in litt.* 1992).

MEASURES PROPOSED (Unless otherwise stated, the points below derive from Snyder *et al.* 1987).

Miscellaneous Insecticidal treatment of parrot nests might be effective against warble-fly parasitism, but may run certain risks to the parrots themselves, so that careful evaluation of this resort should be made before implementation (a study of such treatment using Pearly-eyed Thrashers concluded that additional work was needed to perfect the technique: LaRue 1987). Rat poisoning is questionable in the long term but its value in forestalling the destruction of eggs early in the season before females have developed incubation constancy, and in preventing the loss of eggs or young in the event of the death of a female later in the cycle, justifies continuation until the parrot population shows fuller recovery. Because only one unscrupulous hunter could yet have a serious impact on the population, intensive enforcement of hunting regulations in Luquillo must remain for many years. Long-term vigilance is also needed for the threats of competition and hybridization posed by other amazons introduced into Puerto Rico. Moreover, the growing populations of exotic psittacines on the island need monitoring and perhaps even control (notably at Río Abajo: see below), given their potential for transmitting disease to the native species (J. W. Wiley *in litt.* 1992). Moves to reopen road 191 through Luquillo and to increase cutting of timber there are likely to be detrimental to the parrot's prospects and need to be subject to careful evaluation (J. W. Wiley *in litt.* 1992; again note Remarks 2). The official target is to establish a population of 500 birds in the Luquillo mountains (USFWS 1987).

Reintroduction (at Río Abajo) If the worrying problems in reproduction in the wild are habitat specific and beyond correction, the species can ultimately be saved only by reintroductions elsewhere, something that needs at some stage to happen in any case in order to guarantee its long-term survival. Preliminary reconnaissance suggests that the karst region of the Río Abajo Commonwealth Forest is the most favourable area, as it is an area which the species previously occupied, which can be patrolled well, and in which relatively few Red-tailed Hawks or Pearly-eyed Thrashers occur (against this, however, is the small size of the reserve, its high percentage of edge habitat, and its intensive timber management: F. J. Vilella *in litt.* 1992); a second promising area is the Cristal-Camandules region of lower Luquillo, with many tabonuco, half the rainfall, and few thrashers; six other possible sites, including the offshore islands of Culebra and Mona, deserve consideration (although habitat destruction on Culebra for housing and tourism is perhaps now too extensive, and Vieques would appear a better alternative: J. W. Wiley *in litt.* 1992). It has been recommended that the Río Abajo aviary should be stocked with non-breeding adults and captive-bred juveniles from the Luquillo aviaries, and that no attempts to establish a second wild flock should be made until the existing wild stock exceeds 70 birds, as to do so would conflict with bolstering the extant wild stock as quickly as possible (Wilson *et al.* in press). Studies of wild juveniles have suggested that the optimal time for integration of captive-bred birds into a wild flock would be at around five months (Lindsey *et al.* 1991). The official target is to establish 500 birds in the Río Abajo forest in addition to the 500 at Luquillo (USFWS 1987).

Third captive population on U.S. mainland Following the population viability analysis in 1989, it was recommended that the species's security and propagation might be enhanced by the establishment of a reserve population at a zoo on the U.S. mainland (Lacy *et al.* 1989). However, this move was opposed and finally ruled out on the grounds that it would greatly escalate the risks of disease transmission as well as compound problems of finding good matches amongst prospective mates (Wilson *et al.* in press).

REMARKS (1) As circumstantial evidence of former occurrence in dry forest, at least two congeners, Green-cheeked Amazon *Amazona viridigenalis* and Hispaniolan Amazon *A. ventralis*, the latter a close relative, are now well established in such habitat in southern Puerto Rico, utilizing trees such as úcar *Bucida buceras* and ceiba *Ceiba pentandra* for breeding, these being quite possibly historical nesting trees for the Puerto Rican Amazon since they are common throughout the coastal forests of the country (F. J. Vilella *in litt.* 1992). (2) Luquillo Forest is also a major area for two threatened endemic subspecies of bird, the Puerto Rican Sharp-shinned Hawk *Accipiter striatus venator* and Puerto Rican Broad-winged Hawk *Buteo platypterus brunnescens* (King 1978-1979; see also Snyder *et al.* 1987).