DISTRIBUTION AND BREEDING BIOLOGY OF THE RED-FRONTED MACAW

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ABSTRACT.—The Red-fronted Macaw (*Ara rubrogenys*), endemic to Bolivia with a restricted range and a small population, was observed regularly between late December 1981 and early March 1982. Individuals were found at elevations between 1300 and 2400 m in the arid intermontane valleys of south central Bolivia in southeastern Cochabamba and western Santa Cruz departments, where they had been reported previously, and in northwestern Chuquisaca and northeastern Potosí departments. Seven nests were located in cavities in cliffs 15 to 50 m tall. Courtship and incubation activities took place during December and January. Nestlings were present during February and March. *Received 10 Dec. 1990*, *accepted 28 March 1991*.

The Red-fronted Macaw (*Ara rubrogenys*) is a little-known psittacine, previously reported from the departments (dptos.) of Cochabamba and Santa Cruz in central Bolivia (Forshaw 1978). Carriker collected a male in Oct. 1937 from Ele Ele (Fig. 1; Bond and Meyer de Schauensee 1942, 1943). Romero (1974) captured 10 specimens in 1973 and early 1974 for the live-bird trade from an unnamed valley in Dpto. Cochabamba. R. S. Ridgely (1981, pers. comm.) observed flocks of up to 80 macaws during March and April 1977 in several valleys in western Dpto. Santa Cruz and adjacent Dpto. Cochabamba. Beginning in 1979, Wells (1981) obtained the macaws for aviculture from Valle Grande, 50 km southeast of Pulquina (Fig. 1).

Ridgely (1981) was told by local residents that the macaws nested semicolonially on certain cliffs from September to February. He was shown one inactive site, said to be used by one or two pairs. Wells (1981) mentioned that he observed collectors taking an unstated number of nestlings from burrows in cliffs and that some burrows went about 3 m into the cliffs. There are no other references on nesting Red-fronted Macaws.

I traveled in Bolivia from December 1981 to March 1982. I observed Red-fronted Macaws in various parts of their known range, looked for the macaws in similar habitat outside of dptos. Cochabamba and Santa Cruz, searched for their active nests, and talked with residents familiar with the species.

STUDY AREA AND METHODS

I studied macaws in the arid intermontane valleys along the eastern slope of the Andes in south central Bolivia (Montes de Oca 1982). The high plains ("altiplano") and mountains

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FIG. 1. Map of south central Bolivia showing the departments, localities, and rivers discussed in the text.

("cordilleras") of the Andes are mostly between 3000 and 6000 m elevation. Dissecting the eastern Andes ("Cordillera Oriental") are the ríos Mizque, Grande, Caine, and Pilcomayo, which flow generally to the southeast and east, and the headwaters of the Río Yapacani which flow north (Fig. 1). The drainages form a series of intermontane valleys ("valles") that are at 1000 to 3000 m. Along the eastern edge of the Andes, at 500 to 2000 m, is the discontinuous front range ("Frente Subandino"), with gaps where the major rivers exit the mountains. East of the Andes are the lowland plains ("Llanuras") of southeastern Bolivia.

The substrate of the valley region consists of sandstones, conglomerates, quartzites, and limestones (Montes de Oca 1982). Cliffs are present both near the rivers and farther up on the slopes. Many of the cliffs are poorly cemented sandstones and conglomerates, with numerous cracks and cavities.

The valley region has a warm, relatively dry climate. The area is protected from the moisture-laden winds from the north and northeast by an eastward extension of the Andes north of the Río Mizque (Bond and Meyer de Schauensee 1942, Muñoz-Reyes 1980). Mean annual rainfall in the valleys is between 300 and 800 mm, with the majority coming between November and April (Montes de Oca 1982).

Carriker (in Bond and Meyer de Schauensee 1942) described the vegetation at Ele Ele (1450 m) in Dpto. Cochabamba as thorny scrub with a tremendous variety of cactus, some over 12 m tall. He described the higher slopes above Ele Ele (2450 m) as including a fair number of trees 9–12 m in height. Ridgely (1981) described the habitat in western Dpto. Santa Cruz as desert-like shrubby vegetation in the valleys and on the lower slopes (1300–1500 m) and a somewhat taller, although still dry, woodland on the upper slopes and ridges (2000–2200 m).

Montes de Oca (1982) classified the vegetation in much of the arid intermontane valley

region as temperate and subtropical thorn woodland ("monte espinoso") and dry forest ("bosque seco"), based on the life zone classification developed by Holdridge (1967) and applied to Bolivia (Tosi et al. 1975). Similar areas in the northern valleys are classified as subtropical lower montane thorn steppe ("estepa espinoso") and dry forest (Tosi et al. 1975, Montes de Oca 1982). Common Anacardiaceae include *Lithraea* spp., *Shinopsis* spp., and *Shinus molle*; common Cactaceae include *Cereus* spp., *Neocardenasia herzogiana, Opuntia* spp., and *Trichocereus* spp. (Muñoz-Reyes 1980, Montes de Oca 1982). Other common shrubs and trees of the valley region include *Acacia* spp. and *Prosopis* spp. (Mimosaceae), *Cassia* spp. and *Caesalpinia* spp. (Caesalpiniaceae), *Celtis* spp. (Ulmaceae), *Gourliaea decorticans* (Fabaceae), *Maytenus* spp. (Celastraceae), *Jacaranda acutifolia* (Bignoniaceae), and *Zizyphus* spp. (Rhamnaceae), among many others (Montes de Oca 1982).

The vegetation at the higher elevations within the valley region and to the west of the valley region is mostly subtropical and temperate montane and subalpine forest, steppe, and desert scrub (Montes de Oca 1982). The vegetation in the mountains north, east, and south of the valley region is mostly subtropical and temperate moist forest and wet forest (Montes de Oca 1982). The vegetation of the lowland plains east of the valley region is classified as temperate thorn woodland and dry forest (Tosi et al. 1975, Montes de Oca 1982), similar to the habitat in the arid intermontane valleys.

The arid intermontane valleys are rich in endemic species. Six species endemic to Bolivia are found only in this "Valle zone" of the central Bolivian Andes (Remsen and Traylor 1989): Red-fronted Macaw, Wedge-tailed Hillstar (*Oreotrochilus adela*), Bolivian Earthcreeper (*Upucerthia harterti*), Bolivian Warbling-Finch (*Poospiza boliviana*), Citron-headed Yellow-Finch (*Sicalis luteocephala*), and Bolivian Blackbird (*Oreopsar bolivianus*). Five other species are found only in the dry valleys from northwestern Bolivia south to northern Argentina (Remsen and Traylor 1989): Red-tailed Comet (*Sappho sparganura*), Rufousbanded Miner (*Geositta rufipennis*), Rock Earthcreeper (*Upucerthia andaecola*), Brownbacked Mockingbird (*Mimus dorsalis*), and Rufous-sided Warbling-Finch (*Poospiza hypochondriaca*).

I studied the Red-fronted Macaw during six weeks between late December 1981 and early March 1982. I hiked about 340 km up and down the valleys and canyons along the eastern slope of the Andes. I observed the macaws while walking and camping, and made a few observations while traveling on trucks. An unknown number of macaws were counted more than once; however, the numbers provide a comparison of the relative abundance and activity of the macaws in each area. After locating the macaws at possible nest cliffs, I observed the macaws for one or more days, usually from an observation point 50 to 200 m in front of and below the cliff. The behaviors of the adult macaws and the calls of nestlings indicated the stages of the breeding cycle. I did not carry technical climbing equipment and was not able to examine any nest cavities.

RESULTS

Distribution. — I observed Red-fronted Macaws in flight along the valleys of the ríos Mizque, Grande, and Pilcomayo in dptos. Cochabamba, Santa Cruz, Chuquisaca, and Potosí (Fig. 1). I observed 245 macaws during 18 to 27 December and 27 February to 8 March (203 observation hours [h]) along 50 km of the Río Mizque and a tributary between Saipina, La Junta, and Pulquina (1300–2100 m, Fig. 1). I observed 176 macaws during 4 to 10 January (70 h) along 40 km of the Río Mizque between Peña Colorada and Ele Ele (1450–2100 m, Fig. 1). I saw six macaws on 29 December (2 h) farther up the Río Mizque near Gramal (1800 m, Fig. 1). To the south, I observed 51 macaws on 30 December and 2 January (8 h) along 40 km of a tributary of the Río Grande between Puente Arce and Chaco (1600–1900 m, Fig. 1). I observed 14 macaws during 15 to 17 January (22 h) along 20 km of the upper Río Pilcomayo and a tributary, between Icla and Uyuni (2100–2400 m, Fig. 1). These totals exclude the repetitious observations of nesting pairs under observation. During 305 h of observation time, I observed a total of 492 Red-fronted Macaws: 58 single macaws, 101 pairs, and 45 flocks of 3–12 macaws. Remsen (pers. comm.) observed two flocks of 7 and 50 Red-fronted Macaws in late June 1984 near Tambo, about 10 km north of Pulquina (Fig. 1).

I did not travel farther down into the valleys and canyons of the Río Pilcomayo in the southern half of Dpto. Chuquisaca south of Uyuni. On 9 February, I did travel through areas of dry woodland vegetation and cliffs along a stretch of the Río Pilcomayo and its tributaries in northern Dpto. Tarija, about 240 km southeast of Uyuni. I did not see any Redfronted Macaws, but I did see two pairs of Military Macaws (*A. militaris*) flying along cliffs above the river in the canyon just west of where the river flows out of the mountains and into the lowland plains. I spent two more days travelling in the eastern Andes in Dpto. Tarija but saw no more macaws.

Daily activities away from the nests. — The Red-fronted Macaws were visible and active in the morning (05:30–09:29; $\bar{x} = 1.8$ macaws/h of observation time), around noon (11:30–13:29; $\bar{x} = 1.8$ macaws/h), and again in the late afternoon and evening (15:30–19:29; $\bar{x} = 2.1$ macaws/h). During periods of activity, the macaws were flying up and down the drainages and feeding. I observed the macaws feeding 12 times on fruits of Jatropha hieronymii (Euphorbiaceae), a common tree in the valleys (species identified by D. Wasshausen, pers. comm.). Two macaws were seen eating corn (Zea mays), and one was nibbling on the fruits on the top of a large columnar cactus (Cereus sp.). There were lulls in activity in the late morning (09:30–11:29; $\bar{x} = 1.2$ macaws/h) and afternoon (13: 30–15:29; $\bar{x} = 0.8$ macaws/h), when the macaws were preening and loafing on cliffs or in the vegetation. The two largest flocks (10 and 12 macaws) were observed in the late afternoon and evening and may have been roosting flights.

Nest sites. – I located seven active Red-fronted Macaw nests along the Río Mizque drainage system in southeastern Dpto. Cochabamba and western Dpto. Santa Cruz (Fig. 1). The nest cavities were inside crevices in cliffs composed of sandstones and conglomerates. All cavities were located in sheer or overhung parts of the cliffs. Nest entrances faced northeast (2), east (1), southeast (1), southwest (2), and west (1). The nests

were between 2 and 20 m ($\bar{x} = 9$ m) below the top of the cliff and between 10 and 48 m ($\bar{x} = 18$ m) above the base of the cliff. Three nests were in the top third of the cliff face, and the remaining four were in the middle third of the cliff face. The cliffs were 15 to 50 m tall ($\bar{x} = 28$ m) and 15 to 600 m long ($\bar{x} = 245$ m). The bases of the cliffs were 0 to 300 m ($\bar{x} = 140$ m) above the river and 600 to 1200 m ($\bar{x} = 870$ m) below the top of the ridge. The elevations of the nests were between 1300 and 1800 m ($\bar{x} = 1520$ m).

The two closest Red-fronted Macaw nests were 200 m apart on separate cliffs and two other nests were 500 m apart on separate cliffs. There were two active Blue-fronted Parrot (*Amazona aestiva*) nests and six active Mitred Parakeet (*Aratinga mitrata*) nests in cavities on the same cliffs and within 100 m of active Red-fronted Macaw nests. Monk Parakeets (*Myiopsitta monachus luchsi*) build their stick nests on cliffs (Lanning 1991) and had one nest structure 30 m below an active macaw nest. When the various nesting parrots saw other parrots fly to or near the same or nearby cliffs, they often interacted by vocalizing, perching on the cliffs and nearby vegetation, and flying near the cliffs and near each other.

Breeding behavior. —I observed pairs of macaws in the vicinity of their nest cliffs from dawn to dusk during ten complete days (143 h). I made additional observations during parts of eight days (55 h); the behaviors were similar and appeared to confirm the patterns observed during the complete days.

I observed two days of courtship activity (22 December and 5 January) at two cliffs. One pair spent the preceding and following nights in the cavity, and the second pair spent the nights at an unknown location outside the cavity. One pair was together inside the cavity for two periods during the day, and the other pair was in the cavity seven times during the day. Both pairs regularly perched on the cliffs or in the nearby trees, preened each other, and fed each other (by regurgitation). One pair was observed copulating once, just after the male fed the female. One or both macaws at the two cliffs were in the cavity during 37% of the two days, both macaws were in the vicinity (within 100 m) of the cliff during 22% of the days, and both macaws were gone from the area the remaining 41% of the time.

I observed three days of incubation activity (22 and 24 December and 6 January) at three nests. All three pairs spent the nights in the nest cavity. Each pair copulated once during the day's observations, allowing the male and female to be identified by their behavior and then by individual differences in plumage. Two of the females left the nest seven times throughout the day, and the other female left four times. The females at the three nests left the nest for periods of $3-15 \min (\bar{x} = 8.0 \pm 4.1 \text{ [SD]})$

and were fed by the male, while perched on a limb usually below and in sight of the nest cavity. One or both macaws at the three nests were in the nest cavity during 95% of the three days, and both were within sight of the nest cavity (within 100 m) the remaining 5%. At no time were both macaws gone from the area.

I observed five days of activity during the nestling period (28 February and 1, 3, 6, and 7 March) at three nests. Two adult pairs spent the nights in the nest, and the third pair arrived at the nest cliff 60 min after dawn and left 20 min before dusk. One or both macaws entered each nest 2 to 6 times during the day. Each episode in the nest lasted 14 to 189 min (\bar{x} = 51 \pm 49; N = 18). The nestlings had monotone "nyah" calls that were higher and more nasal than the calls of the adults. I heard "gurgling" sounds while the nestlings were being fed; both adults fed the young. At least two nestlings were audible at each of two of the nests. At the third nest the roar of the river drowned out the calls; however, the activities of the adults were similar to the activities at the other nests. One or both macaws were in the nest cavity during 39% of the five days, both were in the vicinity of the nest cliff (but not inside the nest) during 6% of the days, and both were gone from the area the remaining 55% of the time. I did not see the nestlings make their first flight, nor did I see any young birds flying by the time I left the region on 8 March.

DISCUSSION

Distribution. – I found Red-fronted Macaws in western Dpto. Santa Cruz and southeastern Dpto. Cochabamba, where they had been reported by Bond and Meyer de Schauensee (1943), Forshaw (1978), Romero (1974), Ridgely (1981), and Wells (1981). I also found them to the south in northwestern Dpto. Chuquisaca and the northeastern edge of Dpto. Potosí, where they had not previously been recorded (Remsen and Traylor 1989). Forshaw (1989) included the Río Pilcomayo as part of the macaw's range. All individuals were seen along the three major drainages in the intermontane valley region, at elevations between 1300 and 2400 m above sea level. Local residents said that the macaws were present throughout the year along all three drainages.

There are a few recently published references on the macaw's distribution. Nores and Yzurieta (1984) observed 200 Red-fronted Macaws in October 1982 in a corn field 9 km south of Gramal (Fig. 1). Cordier (in Alderton 1985) observed four Red-fronted Macaws near the Río Mizque during April 1970. C. Cordier (in Alderton 1985) has collected Red-fronted Macaws since 1968 for aviculture and has observed an unlisted number near the Río Caine (Fig. 1). Remsen, Traylor, and Parkes (1986) reported a specimen collected in July 1921 at El Palo, about 25 km east

of Pulquina (Fig. 1). N. J. Collar and N. Krabbe (unpubl. data) have several unpublished specimen records from the Río Mizque and Río Grande drainages.

The arid intermontane valleys inhabited by Red-fronted Macaws are nearly surrounded by terrain and vegetation unsuitable to the macaws (Ridgely 1981, this study). Ridgely (1981) suggested that the macaw's range may extend a short distance to the south of the Río Mizque and Río Grande drainages, and, as he predicted, I subsequently found it in the upper end of the Río Pilcomayo valley. The southern limit of the macaw's range along the Río Pilcomayo is not yet known; however, suitable vegetation exists in a narrow corridor along the valley of the Río Pilcomayo for 250 km to the southeast, where the river exits the mountains and enters the lowland plains.

Nest sites. – I found Red-fronted Macaws nesting in cavities in cliffs in western Dpto. Santa Cruz and southeastern Dpto. Cochabamba. Suitable nest sites in cliffs appeared to exist in the canyons and rugged valleys throughout the known range of the macaw. Although several large macaws nest in tree cavities, I did not find any trees in the arid intermontane valleys that could provide nest cavities large enough for the Red-fronted Macaw. The Red-fronted Macaw's cliff nest sites are similar to the cliff nests of some other psittacines, including the Indigo Macaw (Anodorhynchus leari, Sick 1981), Military Macaw (Gardner 1972, Ridgely 1981), Scarlet-fronted Parakeet (Aratinga wagleri; Meyer de Schauensee and Phelps 1978, Ridgely 1981), and the Maroon-fronted Parrot (Rhynchopsitta terrisi, Lawson and Lanning 1981).

Status. – Ridgely (1981) estimated that the total population of Redfronted Macaws was no more than 1000–3000 birds in an area about 100 km from west to east and 50 km from north to south. The macaw's range is now known to be unevenly dispersed over a 150 km by 180 km area (Fig. 1). Combining Ridgely's estimate of population size and range with current information on the macaw's range and habitat, I estimated that there were 3000 to 5000 Red-fronted Macaws in the wild (Lanning, unpublished report to the International Council for Bird Preservation and New York Zoological Society in 1982). C. Cordier (in Silva 1989) feels that "5000 is a reasonable figure," but suggested that "aggregates were large prior to ravages by bird dealers."

The major threat to the species during the 1970s and 1980s was trapping of up to several hundred macaws annually for exportation to the U.S., Europe, and Japan (Ridgely 1981).

In July 1983 the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed the Red-fronted Macaw in Appendix I, effectively limiting and regulating exportation and importation among countries participating in the Convention (Jorgenson and Thomsen 1987). In May 1984, the Bolivian government banned the export of all live wildlife (Jorgenson and Thomsen 1987). However, in October 1984, "surreptitious specimens" could be purchased in Bolivia, and were reportedly being exported abroad in very small numbers from an "adjacent" country (Silva 1989). No Red-fronted Macaws have legally entered the United States since 1983 (Jorgenson and Thomsen 1987, Silva 1989). Silva (1989) believed that the CITES listing should offer some protection from the "ravages of unscrupulous dealers," and the Bolivian government export ban on wildlife was officially extended to at least June 1989 (Gaski 1987).

Now that the species is officially protected from exportation for the live-bird trade, other threats to the continued health of the species may have increased in importance and need to be considered during future studies. Current threats may include direct persecution by residents and by farmers protecting their corn and peanut crops (Romero 1974, Wells 1981, Alderton 1985), the continuing illegal capture and trade of live macaws (Silva 1989), and habitat destruction (Cordier, in Alderton 1985).

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