Spatial ecology and conservation of the endemic and endangered Red-fronted Macaw (*Ara rubrogenys*) in the Bolivian Andes

Diploma Thesis

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Abbreviations

°C	degrees Celsius
#	number
%	per cent
A.	*Ara*
cm	centimetres
Fig.	figure
g	grams
GPS	global positioning system
ha	hectares
IIL	independent individual location
km	kilometres
km^2	square kilometres
m	meters
MCP	minimum convex polygon
min	minutes
mm	millimetres
No.	number
Nov.	November
Oct.	October
OHR	overall home range
PTT	Platform Transmitting Terminal
RF	radio frequency
SFDRA	seasonal feeding and daytime roosting area
SHR	seasonal home range
Sept.	September
sp.	species
US$	US Dollars

Abstracts

Abstract

The Red-fronted Macaw (*Ara rubrogenys*) is en endangered species endemic to the inter-Andean dry valleys of Bolivia. In order to augment the knowledge of the species' spatial ecology, we tracked nine Red-fronted Macaws using radio telemetry between August 2008 and January 2010. Only one macaw yielded sufficient independent locations for home range estimation. Reliable estimates for seasonal home range sizes ranged between 330 ha and 5738 ha. The macaw showed a marked migration pattern and site fidelity for a seasonal winter home range in the easternmost part of the species' range. Minimum daily covered distances ranged between 9 km and 28.5 km. The macaw moved widely over the year but was seasonally restricted to rather small areas, indicating that both local and landscapes aspects are important for the species' conservation. More generally, macaws aggregated in flocks of more than 200 individuals on winter feeding grounds. In the winter home ranges we encountered night roosts in narrow valleys with high forest. Although most conclusions are based on one individual, circumstantial evidence indicates that several of the observed movement patterns may be representative for a large part of the global population of the species. Several conservation-related statements in the published and unpublished literature on Red-fronted Macaws are based on unwarranted assumptions and are discussed critically. Demographic studies and monitoring of the global population are recommended. In conclusion, despite our low success rate in gaining radio telemetry data, we were able to further clarify certain aspects of the spatial ecology and the conservation of the species.

Resumen

La paraba frente roja (Ara rubrogenys) es una especie en peligro de extinción que es endémica para los valles secos interandinos de Bolivia. Para aumentar los conocimientos sobre la ecología espacial de la especie utilizamos radio-telemetría para seguir nueve parabas frente roja entre agosto de 2008 y enero

de 2010. Sólo una paraba aportó suficientes locaciones para estimaciones fiables de rangos de hogar. Estimaciones fiables de rangos temporales de hogar variaron entre 330 y 5738 hectares. La paraba mostró marcados patrones de migración y fidelidad para un rango de hogar de invierno en el extremo este del área de distribución de la especie. Mínimas distancias cubiertas durante un día variaron entre 9 y 28.5 kilómetros. La paraba se movió extensamente durante todo el año pero estaba temporalmente restringuida en áreas bastante pequeñas, indicando que ambos aspectos locales y aspectos del paisaje son importantes para la conservación de la especie. En general, parabas se agregaban en bandadas de más de 200 individuos en los lugares invernaderos de alimentación. En los rangos de hogar de invierno encontramos dormideros en valles estrechos con bosque alto. Aunque la mayoría de las conclusiones está basada en un individuo, evidencia circunstancial indica que varios de los patrones observados de movimiento podrían ser similares para una gran parte de la población mundial de la especie. Varias declaraciones relacionadas a la conservación en la literatura publicada y no publicada están basadas en suposiciones no justificadas y están críticamente discutidas. Estudios demográficos y monitoreo de la población mundial estan recomendados. En conclusión, pese a nuestra baja tasa de éxito consiguiendo datos de telemetría, pudimos aclarar ciertos aspectos de la ecología espacial y de la conservación de la especie.

Zusammenfassung

Der Rotohrara (Ara rubrogenys) ist eine vom Aussterben bedrohte Art, die endemisch in den interandinen Trockentälern Boliviens vorkommt. Um den Wissensstand über die räumliche Ökologie dieser Art zu erweitern, haben wir zwischen August 2008 und Januar 2010 neun Rotohraras mit Hilfe von Radiotelemetrie verfolgt. Nur von einem Ara konnten genügend Aufenthaltsorte für zuverlässige Abschätzungen der saisonalen Bewegungsareale erfasst werden. Zuverlässige Abschätzungen der saisonalen Bewegungsareale reichten von 330 ha bis 5738 ha. Der Ara zeigte ein ausgeprägtes Migrationsmuster und Ortstreue für ein Überwinterungsgebiet im östlichsten Teil des Verbreitungsgebietes der Art. Minimale täglich zurückgelegte

Distanzen reichten von 9 bis 28,5 Kilometer. Der Ara bewegte sich im Jahresverlauf über weite Distanzen, war jedoch saisonal auf vergleichsweise kleine Gebiete beschränkt, was Hinweise darauf gibt, dass sowohl lokale als auch Landschaftsaspekte für den Schutz der Art wichtig sind. Es fanden sich Schwärme von über 200 Aras über den winterlichen Fressplätzen zusammen. Wir haben in den Überwinterungsgebieten Schlafplätze in engen Tälern mit hohem Wald entdeckt. Obwohl die meisten Schlussfolgerungen nur auf einem Individuum basieren, legen verschiedene Indizien den Schluss nahe, dass einige der beobachteten Bewegungsmuster repräsentativ für eine großen Teil der globalen Population dieser Art sein könnten. Verschiedene Naturschutz-relevante Aussagen in der publizierten und nicht publizierten Literatur über Rotohraras basieren auf ungerechtfertigten Annahmen und werden kritisch diskutiert. Demographische Untersuchungen und die Überwachung der Bestandsentwicklung der globalen Population werden empfohlen. Zusammenfassend war es uns möglich, trotz unserer geringen Erfolgsrate bei der Gewinnung von Telemetrie-Daten einige Aspekte der räumlichen Ökologie und der Naturschutzbiologie der Art weiter aufzuklären.

1. Introduction

1.1. Natural history of the Red-fronted Macaw

1.1.1. Identification

With a size of about 60 cm, the Red-fronted Macaw (*Ara rubrogenys*) is the smallest member of the genus *Ara*. Its general plumage is olive green, with a striking red forehead, crown and spot behind the eye. Certain parts of the wings and tail are orange, olive-yellow and blue, and are especially conspicuous during flight (Fig. 1). The juveniles are generally duller and become brighter as they grow older. Males have shorter wings and tails than females but are heavier (Forshaw 1989).

Fig. 1: A pair of Red-fronted Macaws perched in a dead tree. Picture taken near Pampagrande.

1.1.2. Evolution

A. rubrogenys is the sister species of a group formed by [(*A. militaris* + *A. ambigua*) + (*A. macao* + *A. chloroptera*)] and diverged from that group during the Pleistocene (Miyaki & Ribeiro de Oliveira-Marquez 2006).

1.1.3. Feeding

Red-fronted Macaws are seasonally specialized on different food plants. These include *Cenchrus* sp. (Poaceae), *Jatropha* sp. (Euphorbiaceae), *Schinopsis haenkeana* and *Loxopterygium* sp. (Anacardiaceae), *Ziziphus mistol*

(Rhamnaceae), *Prosopis* spp. (Mimosoideae), *Apidosperma* sp. (Apocynaceae), *Tipuana* sp. (Faboideae), and possibly *Cereus* sp. and *Neocardenasia* sp. (Cactaceae). In addition to natural food plants, macaws feed heavily on cultivated maize and peanuts (Boussekey *et al*. 1991, Clarke & Duran-Patiño 1991, Pitter & Christiansen 1995).

1.1.4. Behaviour

Red-fronted Macaws are semi-gregarious (Lanning 1982), flying singly, in pairs or in flocks. Reported flock sizes range between up to twelve (Lanning 1982) and up to 90 (Pitter & Christiansen 1995). Cohesion within pairs is very strong and pair bonds are maintained throughout the year by social interactions such as allopreening, courtship feeding and copulations (Pitter & Christiansen 1997). Although the macaws usually roost and feed in flocks, social interactions mostly take place within pairs, between parents and their offspring or among juveniles. Entire flocks do, however, communicate regularly by vocalizing or performing synchronous movements (Pitter & Christiansen 1997). Aggression is rare in Red-fronted Macaws, although breeding pairs can be dominant over non-breeding birds and defend breeding sites (Pitter & Christiansen 1993b).

Red-fronted Macaws nest semi-colonially in crevices and cavities in tall sandstone cliffs from November to March (Ridgely 1981). Only the female incubates the eggs, but the male will spent much time with the incubating female and sometimes roost in the nest hole with the female (Lanning 1991). Breeding pairs usually rear between one and two and occasionally even three chicks per year (S. Herzog, pers. comm.). Both parents participate in the care for the fledglings (Christiansen & Pitter 1993a). Juveniles remain with their parents at least until the following breeding season (Christiansen & Pitter 1993a).

The macaws are most active in the early morning and late afternoon and also feed primarily during these periods. They spent much of the hotter times of the day resting in cliffs or tall trees, where they engage in social interactions (Lanning 1991). They usually follow a set pattern of activities and return to the same night roosts each evening (Pitter & Christiansen 1995).

1.1.5. Distribution

The Red-fronted Macaw is endemic to the inter-Andean dry valleys of the east Andean slope in central Bolivia, from southern Cochabamba and western Santa Cruz through northern Chuquisaca and north-eastern Potosí. Its range extends over an area of approximately 10,100 km² where it is principally found in the valley systems of the Ríos Caine, Mizque, and Pilcomayo (Lanning 1982, BirdLife International 2010) (Fig. 2).

1.1.6. Spatial ecology

Little is known about movement areas of Red-fronted Macaws. Pitter & Christiansen (1995) estimated that a breeding population in the Caine valley had a home range of ca. 5,000 hectares. The Red-fronted Macaw was considered resident by Lanning (1982) and Pitter and Christiansen (1995), whereas other studies (Clarke & Duran-Patiño 1991, Herzog *et al*. 1997) have questioned that.

Observations by Armonía (see below) suggest that by late March most adults and their young of the year leave the breeding areas and migrate to largely cultivated regions in more humid dry valleys generally to the north and east of the breeding areas, presumably because of greater food availability on agricultural fields. A small number of birds (apparently adults that did not reproduce in a given year) remain in breeding areas year-round (S. Herzog, pers. comm.).

1.2. Conservation

1.2.1. Conservation of parrots

Parrots (Psittacidae) are among the most highly threatened birds in the world, with more endangered species than any other bird family (Collar *et al*. 1994). Most New World parrot species are experiencing declines in numbers (Collar & Juniper 1992, Collar 2000), with at least 51 of the 161 species (31.7 %) regarded as threatened and a further nine already extinct (IUCN 2010).

Although a number of factors are implicated in the global decline of parrot populations, two are considered of primary importance: habitat loss and the capture of individuals for the pet trade (Collar & Juniper 1992, Juniper & Parr 1998, Snyder *et al*. 2000). The study of parrots is a conservation priority and the Association for Parrot Conservation (APC) and the IUCN Parrot Conservation Action Plan recommend monitoring psittacine populations (Beissinger *et al*. 1994, Snyder *et al*. 2000).

1.2.2. Conservation of the Red-fronted Macaw

1.2.2.1. Legal status

The Red-fronted Macaw was placed on Appendix I of CITES in 1983. All capture, transport and export of Bolivian wildlife was prohibited by Supreme Degree 21312 of 27 June 1986 (Fuller & Gaski 1987). However, this law is rarely enforced (Herrera & Hennesey 2007).

1.2.2.2. Conservation status

Because the study of Red-fronted Macaws is difficult due the inaccessibility of much of their range, little is known about the status of the Red-fronted Macaw. It is classified as Endangered by the IUCN (BirdLife International 2008). It was described as locally common in most parts of its range visited by Pitter and Christiansen (1995), but most population estimates are both wide and highly speculative. Published estimates range between 1000-3000 (Ridgely 1981), 2000-4000 (Pitter & Christiansen 1995), and 3000-5000 (Lanning 1982, 1991). Clarke and Duran Patiño (1991) made extensive surveys and extrapolated their counts to a population of 555-626 individuals for their study area, with an estimated global population of less than 1000 individuals. Counts of active and potential nests by Armonía resulted in a conservative estimate of 264-579 reproducing individuals, and Armonía considers 700-800 individuals a reasonable estimate for the global population (S. Herzog, pers. comm.).

1.2.2.3. Population trend

As no strict monitoring has been in place for the species so far, there is little reliable information on population trends of the Red-fronted Macaw, although there is a general consent that the global population is declining (Clarke & Duran-Patiño 1991, BirdLife International 2008, 2010).

1.2.2.4. Threats

An estimated 40% of the species' natural habitat in the valleys had been converted to agricultural lands by 1991, with remaining areas being degraded by intensive grazing (Clarke & Duran-Patiño 1991). Several important food trees are harvested for fuel and charcoal. Cultivation is expanding at the expense of natural forests and food plants, which according to Pitter and Christiansen (1995) has lead to the species' seasonal dependence on crops.

After heavy trapping for the pet trade in the early 1980s (Ridgely 1981, Lanning 1982), trapping has become less severe since the species has been afforded legal protection in Bolivia and internationally in the mid-1980s. Most authors believed trapping to be less of a threat during the 1990s (Lanning 1991, Boussekey *et al*. 1991, Clarke & Duran-Patiño 1991, Pitter & Christiansen 1995), but a recent pet trade study revealed that an estimated 100 Red-fronted Macaws a year are traded illegally on Bolivian pet markets (Herrera & Hennessey 2007).

Another potential threat is direct persecution as a crop pest, and Brace *et al*. (1995) documented the use of firearms for pest control. Ridgely (1981), Lanning (1982), and Boussekey *et al*. (1991) argue that there is no systematic persecution, whereas Pitter & Christiansen (1995) and Clarke & Duran-Patiño (1991) afford this threat some, albeit little, importance.

Clarke & Duran-Patiño (1991) report locals' claims that former breeding cliffs have been abandoned by macaws because of human disturbance. Christiansen and Pitter (1993b) on the other hand report that despite much disturbance at breeding cliffs, macaws pay little attention to it. Macaws are also relatively tolerant of human disturbance when feeding on agricultural fields (Boussekey *et al*. 1991, Pitter & Christiansen 1995).

1.2.2.5. Conservation measures under way

The most important protected area in the region is the Torotoro National Park, which protects breeding sites of Red-fronted Macaws along the headwaters of the Río Caine. Non-breeding birds occur in the southern edge of Amboró National Park (S. Herzog, pers. comm.). The Important Bird Area “BO008 - Cuencas de Ríos Caine y Mizque” falls within the species` range (BirdLife International 2009). 5,000 posters urging the protection of Red-fronted Macaws and their habitat were distributed and apparently well received throughout the region (S. Herzog, pers. comm.)

Asociación Civíl Armonía coordinates most research and conservation activities for the species since 2003. They are running a long-term conservation project at the largest known breeding colony in Perereta on the Rio Mizque (20-25 active nests), working with three communities to protect breeding cliffs. An ecotourism lodge was established there, proceeds of which go to the local communities, and it is planned to establish a protected area at this site (S. Herzog, pers. comm.).

1.3. Justification of this study

Despite extensive earlier studies on the distribution and behaviour of Red-fronted Macaws (Ridgely 1981, Lanning 1982, 1991, Boussekey *et al*. 1991, Clarke & Duran-Patiño 1991, Christiansen & Pitter 1993 a, b, Pitter & Christiansen 1995, 1997), some central aspects of their ecology that are important for assessing and monitoring the conservation status of the species as well as much about the factors that limit its global population remain unknown. In particular, much of their spatial ecology, including home ranges, migration/residency, site fidelity, and connectivity between sub-populations, is largely unknown. None of the above studies has included field work during the driest period from April to August, and much of what is published on this matter is mostly based on speculations and has to be treated with great caution.

To clarify these remaining questions, Armonía started a pilot telemetry project in mid-2008, which aimed at studying the movement patterns of nine radio-collared Red-fronted Macaws and was intended to be continued and expanded

if successful. The results of this study were to augment the knowledge of the ecology, allow realistic status assessments, and be the basis for strategies for the conservation and management of Red-fronted Macaws.

I present the results from this study and discuss certain aspects of the species' ecology and conservation, based on a critical review of published and unpublished literature and our own field observations.

2. Study area

2.1. Location

The study area is situated in the arid intermontane valleys (”Valles“) in the eastern Andes of central Bolivia (Montes de Oca 1982). The area lies roughly between the departmental capital cities of Santa Cruz de la Sierra, Cochabamba, and Sucre. Most field work was carried out in the provinces of Florida, M.M. Caballero, and Vallegrande of western Santa Cruz department.

2.2. Climate

The “Valles” region has a warm, relatively dry climate with temperatures between 0°C and 30°C, and a mean annual temperature of 12-16°C (Ibisch *et al*. 2003a). The area is protected from the moisture-laden winds from the north and northeast by an eastward extension of the Andes north of the Rio Mizque (Muñoz-Reyes 1980). Mean annual rainfall in the valleys is between 300 mm and 800 mm, with the majority falling between November and April (Montes de Oca 1982) and six to eight dry months (Ibisch *et al*. 2003a).

2.3. Topography, hydrology and geology

Dissecting the eastern Andes (“Cordillera Oriental”) are the ríos Mizque, Caine, Grande, and Pilcomayo, which flow generally to the southeast and east, and the headwaters of the Río Yapacaní which flow north. The drainages form a series of intermontane valleys at 1000-3000 m. Along the eastern edge of the Andes, at 500-2000 m, is the discontinuous front range (“frente subandino”), with gaps where the major rivers exit the mountains. The substrate of the dry valleys consists of sandstones, conglomerates, quartzites, and limestones. 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 (Montes de Oca 1982).

2.4. Vegetation

The vegetation of the area has been classified by Montes de Oca (1982) as temperate and subtropical thorn woodland ("monte espinoso"), dry forest ("bosque seco"), and suptropical lower montane thorn steppe ("estepa espinosa"). The dominant ecosystem in the study area is usually referred to as inter-Andean dry forest ("bosque seco interandino"), which is comprised mostly of dry deciduous forest with tree heights of 10-20 m (Ibisch *et al*. 2003a), while patches of semi-deciduous and evergreen forest can be found in the river valleys (Pitter & Christiansen 1995). Small parts of the area are comprised of Tucuman-Bolivian forest ("bosque Tucumano-Boliviano") and montane chaco ("chaco serrano") (Ibisch *et al*. 2003a) (Fig. 2).

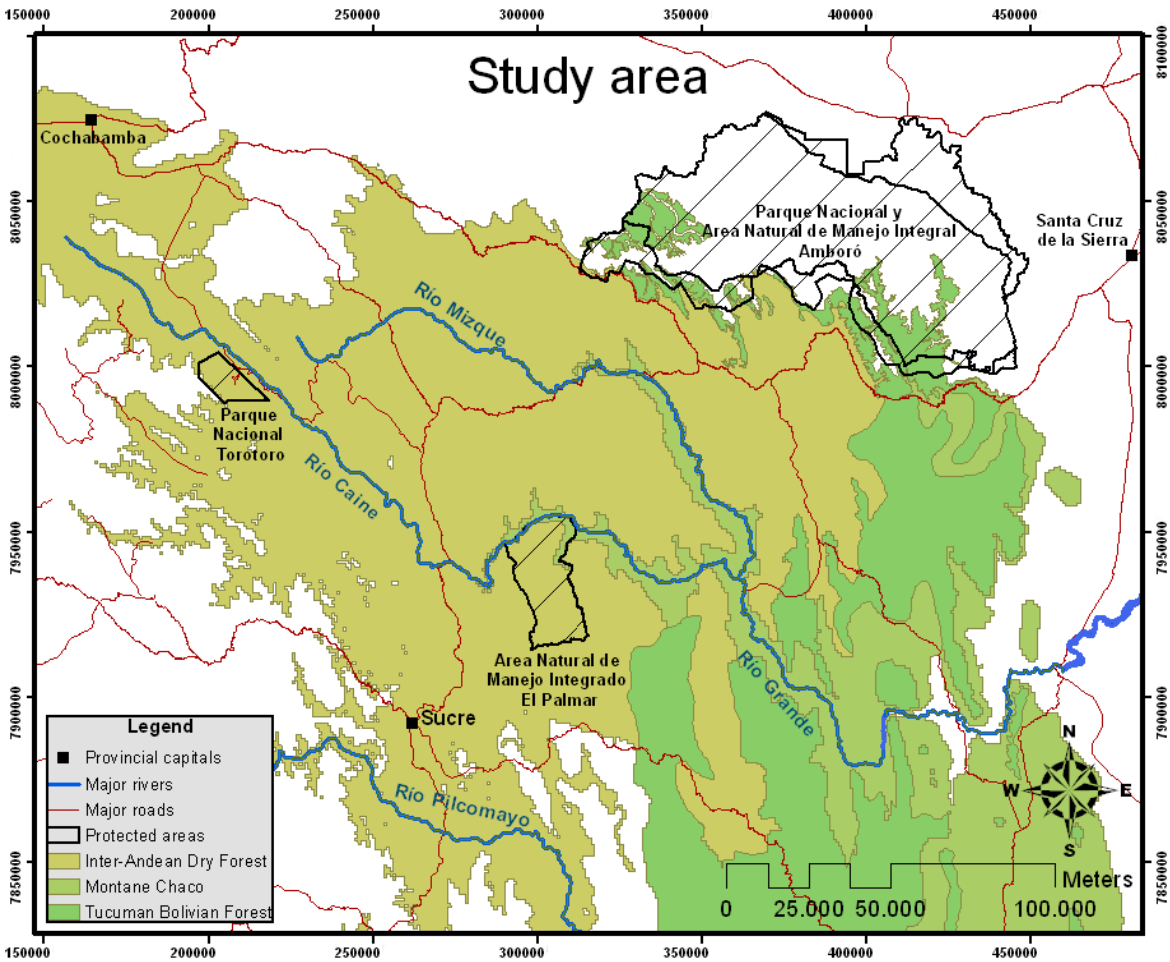


Fig. 2: Map of the study area showing the extent of ecoregions and major protected areas. Only ecoregions were *Ara rubrogenys* has been recorded are shown. The Red-fronted Macaw is distributed principally in suitable habitat near the four main river systems. Ecosystems layer from Ibisch *et al*. 2003, all other geographic features from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).

2.5. Flora

The inter-Andean dry forests can be defined floristically by the following taxa: thorny mimosoid legumes (*Prosopis*, *Acacia*); columnar cacti of the genera *Trichocereus*, *Cleistocactus*, and *Neocardenasia*; Cactaceae with other growth forms of the genera *Opuntia*, *Parodia*, *Rebutia*, and *Weingartia*; Anacardiaceae such as *Schinopsis haenkeana* and *Schinus molle*; *Bougainvillea spinosa* and *B*. *berberidifolia* (Nyctaginaceae); and *Aspidosperma quebrachoblanco* (Apocynaceae) (Larrera-Alcázar & López 2005).

2.6. Biological significance of the inter-Andean dry forests

Ibisch *et al*. (2003a) describe the inter-Andean dry forests as naturally fragmented and very heterogeneous with distinct biogeographic affinities, and as a centre of endemic species diversity for many groups of organisms. The ecosystem boasts a high level of plant species endemism (Antezana & Navarro 2002, López 2003, Wood *et al*. 2006) as well as several endemic vertebrates (Embert 2002, Gonzáles & Reichle 2003, Herzog 2003, Salazar-Bravo & Emmons 2003). Despite the high endemism levels, the inter-Andean dry forests are poorly represented in the Bolivian protected area system (Larrea-Alcazar & Lopez 2005, López & Zambrana-Torrelio 2005).

2.7. Degradation of habitat

The inter-Andean dry forests are one of the most degraded ecosystems in Bolivia (Ibisch *et al*. 2003b), partly because of millennia of use by agrocentric cultures at an elevated population density (Ibisch *et al*. 2003c). Principal causes for continued degradation are increasing demands for agricultural land as well as firewood for domestic and industrial use (Pitter & Christiansen 1995, Clarke & Duran Patiño 1991). Small agricultural fields now occupy most suitable areas along the riverbeds so forest is mostly concentrated on the hillsides and in the steeper valleys. According to local observers, wood-use is inefficient, with forested areas often being burned for agricultural expansion without using the

wood in any way (A. Langer, pers. comm.). Ground cover and regeneration are seriously impaired by overgrazing by cattle and goats (Pitter & Christiansen 1995). The landscape consequently consists of a mosaic of agricultural land, scrubby areas and forest heavily influenced by the activities of humans and their domestic animals (Pitter & Christiansen 1995) (Fig. 3).

Fig. 3: Habitat degradation along the Rio Mizque. Natural vegetation in the valley floor is largely replaced by agricultural fields (background), ground cover is degraded by overgrazing (foreground). Picture taken at the breeding cliffs near Perereta.

3. Methods

3.1 Field work

Most of the data that are presented in this study were collected by ornithologists of Armonía. I carried out data collection with their assistance from early April 2009 to mid-June 2009 as part of the larger study. The data analysis is based on the entire dataset collected between August 2008 and January 2010. During my time in the field, I took notes on any Red-fronted Macaws observed throughout the study area and I regularly counted observed flocks. I photographed some very large flocks to accurately count them afterwards.

3.1.1. Baiting and trapping

The macaws were baited to bait stations on agricultural fields. Peanuts and maize were used as bait. Experience showed that a combination of clearly visible bait stations, absence of disturbance (such as humans or domestic animals) and a configuration of suitable perches (mostly large trees) is crucial for the bait stations to be accepted.

The traps were built of an iron grid of about 2x4 meters to which nylon nooses were attached. This trap design essentially is a modified Bal-chatri trap, which is commonly used to capture raptors (Berger & Mueller 1959). The grid was covered with earth, and the nooses were erected to activate the trap after scattering peanuts across the bait station. The trap was only activated when the observers were convinced that the macaws were not suspicious of the bait stations anymore. The macaws would first perch in nearby trees, then fly down near the bait station and eventually walk onto it, trapping themselves in the nylon nooses.

After successful trapping body masses and morphometric data of the birds were taken and they were equipped with AI-2C collar attachment radio transmitters manufactured by Holohil Systems (http://www.holohil.com/parrot.htm) before release. The weight of the transmitters is 22.5g (between 3.4% and 4.5% of the body mass of the equipped birds) and thus falls within the recommended range of 3-5%

(Caccamise & Hedin 1985, Calvo & Furness 1992). They last between 12 and 30 months (nominal lifespan 24 months) according to the manufacturer.

3.1.2. Radio-tracking

We monitored the radio-collared birds with standard radio tracking techniques (White & Garrott 1990), using a TRX-16S receiver and a 5-element Yagi directional antenna from Wildlife Materials (www.wildlifematerials.com). When we covered large distances by 4x4 vehicle, we attached the antenna to the roof of the car and checked for signals while driving. Additionally, at high points we searched the area thoroughly with the antenna in hand and sometimes we climbed hills for this purpose. Two overflights of the area were undertaken in search of signals, on 14 January 2009 and on 16 December 2009. Coordinates were taken with a Garmin GPS device.

Data collection was either performed by a single observer or, more commonly, by a team of two observers. From 28 August 2008, when the first 5 macaws were trapped, data was collected opportunistically. Other investigators have employed strict sampling regimes, such as three daily fixes, each during a predefined period of the day (e.g. Myers & Vaughan 2004). For logistic reasons we could not maintain such a sampling regime, but we tried to record locations as often as possible and at different times of the day. I pooled sampling times of day into five equal time periods and made histograms of the frequency distribution of the locations to see whether there has been a sampling bias for certain times of the day (see Results). On several days we tried to follow one macaw in order to record locations hourly for analysis of minimum daily covered distances.

We separated consecutive recordings of the locations of the birds by at least 60 min intervals to avoid autocorrelation (White & Garrot 1990). Red-fronted Macaws are powerful flyers with an estimated normal flight speed of up to 60 km/h (Boussekey *et al*. 1991), so we regarded 60 min as a time sufficient to allow a bird to move anywhere within its seasonal home range and therefore considered the locations independent (White & Garrott 1990).

Our principal method of data collection was ‘radioassisted surveillance’ (Harris *et al*. 1990) or ‘homing in’ (White & Garrott 1990), in which the radio equipment

is primarily used to find the birds in the field, and once located they are observed directly. I calculated their estimated locations from the coordinates of the observer's location, the bearing and the estimated distance to the birds using trigonometry. This method has the advantage of being more exact than triangulation but the obvious disadvantage of one having to manoeuvre through difficult terrain and the possibility of disturbing the birds (White & Garrott 1990).

If the birds could not be observed directly, we used triangulation to estimate their locations. In this method, bearings to a radio-tagged animal are estimated with a hand-held compass from at least two different points. The intersection point of the bearing lines is the estimated location of the animal. This method has the advantage that it is possible to locate objects from a greater distance but it has the disadvantage of being less exact and therefore resulting in a higher error ratio (White & Garrott 1990).

When we used triangulation, we took bearings from two points for estimation of each location over a time span of usually 1-10 min (maximum 20 min). Receiver locations were at least 100 meters apart (Keurighlian *et al*. 2004). To estimate the best bearing, we used the strongest signal method (Springer 1979).

3.1.3. Estimation errors

It has been shown that locations tend to be much more exact when more than two bearings are taken for each location (Springer 1979, White & Garrot 1990). Especially when only one team carries out the triangulation with a time interval of several minutes between the bearings (which was the case in our study), the animal can change its position between the bearings, and the error ratio can be particularly high (D. Zinner, pers. comm.).

To calculate location error in the study, I placed four transmitters in the area at known locations. Bearings to these transmitters were taken by A. Paca who was not "blind" to the test (i.e. she knew she was being tested) instead of the "blind" test recommended by Mills and Knowlton (1989). I calculated error as the deviation of the estimated from the true location (Springer 1979, Hupp & Ratti 1983).

In the accuracy test for the triangulation data, one estimate was nonsensical (no crossing of the bearing lines), the three others showed a mean deviation from the actual location of 550.56 meters (SD 76.59) at a mean distance of 754.58 meters (SD 403.52) between the object and the observer.

Other authors have used more test transmitters for testing accuracy of the triangulation data, with the smallest number I found in the literature being 16 (Keuroghlian *et al*. 2004, Mildenstein *et al*. 2005). Unfortunately, we have only tested with four test transmitters, one of which resulted to be nonsensical (N = 3), so any statistical evaluation of accuracy would be pointless (White & Garrott 1990).

To nevertheless get an idea of the potential effect of these estimation errors on home range estimates I created artificial datasets which I considered in the home range analyses (see below). In these datasets I moved the triangulated points by 550.56 meters (the mean deviation) closer to and farther from the home range centre, respectively. I treated the direct observation points in a similar fashion, i.e. by adding and subtracting 20% (which I consider a likely estimation error) to and from the estimated distances, respectively, wherever they exceeded 200 meters.

One possible way of treating the problem of inaccurate estimation from triangulation is to exclude all extreme triangulation data (i.e. locations at the edge of the movement areas) from the analyses, as suggested by White & Garrott (1990). Another effect of eliminating these outliers would usually be eliminating “non-normal” movements of the animal from the analyses (see below).

However, in this study the triangulation data was of particular interest. Triangulation was necessary only when direct observation of the birds was not possible. Precisely for that reason, these data usually provided ‘new’ locations which were different from the ones obtained by direct observation (e.g. hidden side valleys where the presence of the birds had not formerly been recorded). Likewise, the bulk of data obtained by direct observations is likely biased towards the more accessible inner valleys. To counter this bias and to include the valuable extra information, I decided to include most of that triangulation data in the analysis despite the higher error ratio.

The observed pattern that several clusters of locations are separated by larger areas without any locations (see below) was not weakened by the inclusion of most triangulation data except for one fix more then 13 kilometres away from the point from where the bearing was taken. This cannot represent a valid location of a bird as the receiver cannot receive signals at such great distances in the rugged terrain. Rather, it was the result of a very small deviation between the two bearing angles of just 4 degrees. When bearing angles are that close, even a small bearing error of just one or two degrees can result in a very large deviation between the estimated and the actual location of the object (White & Garrott 1990). To minimize this source of error, I excluded all locations where the two bearing angles differed by less then 20 degrees (including the above-mentioned particularly anomalous one) from the analyses.

3.2. Data analysis

I conducted all geographic analyses (minimum covered distances, home ranges, etc.) with ArcGIS Desktop 9.2 (ESRI 2005), mostly using Hawth's Tools Extension (Beyer 2004), except for means with standard deviations of minimum covered distances and calculations of the estimated locations of the macaws from the direct observation and triangulation data, both of which I conducted with MS Excel (2003). A thorough discussion of techniques for estimating animal locations from radio-tracking data is given by White and Garrott (1990).

I plotted the macaws' locations on a map (Instituto Nacional de Estadística, Bolivia, http://www.diva-gis.org/gData), and in the case of the seasonal ranges on a Landsat satellite image (USGS/Glovis). To see in what habitat types the seasonal home ranges were established, I also plotted locations on a vegetation map (Navarro & Maldonado 2002).

I made all statistical tests with R (R Development Core Team 2010). Before tests, I always checked for normal distribution of the respective dataset using Shapiro-Wilk tests (Shapiro & Wilk 1965). I used R, MS Excel, and GraphPad prism 5.0 (www.graphpad.com) to plot results, and Adobe Photoshop CS3 to visualize the concept of the cophenetic correlation (see below).

3.2.1. Home ranges

After loading the tracking locations into ArcMap, it was easily noticeable that the locations were concentrated mainly in three clusters (along with several single points), one each in the Anamal, Pampagrande, and Pulquina areas.

When projected on a map, these defined areas appeared rather small and compact in comparison to the larger distances between such areas. Also, it appeared that continued time series of tracking locations with small enough intervals to assure that the birds had not moved afar during intermediate periods were always restricted to one such cluster and never included two or more of the clusters. On the other hand, locations of one cluster were always separated from tracking locations of another cluster by longer periods with no tracking locations. Therefore, a home range analysis across the different clusters will yield a highly unreliable result, as there remains the uncertainty of where the birds were during the periods between the clusters. I therefore concluded that the animals spent a certain time in one defined area until they eventually moved on to another such defined area. A special case was Pampagrande, where the cluster of locations could be divided into two time periods, one in 2008 and one in 2009, divided by a longer time period during which the other locations were recorded. I therefore decided to analyse four clusters of locations separately (Anamal, Pampagrande 2008, Pampagrande 2009, and Pulquina) and treat each cluster as a separate seasonal home range for that particular time period, in addition to the (unreliable) overall home range for the whole study period (Fig. 8).

An often used polygon for home range estimation is the minimum area polygon (Mohr 1947). It is constructed by connecting the outer locations to form a convex polygon. Other increasingly popular methods for home range estimation are harmonic mean and kernel methods. Boulanger and White (1990) demonstrated that other popular home range estimators perform more poorly than the harmonic mean, while several authors consider kernel estimators more accurate home range estimates than harmonic mean or minimum convex polygon (MCP) models (Naef-Daenzer 1993, Worton 1995, Swihart & Slade 1997, Powell 2000, Pimley *et al*. 2005, Börger *et al*. 2006).

The MCP model has several limitations (Harris *et al*. 1990, Powell 2000, Börger *et al*. 2006, Nilsen *et al*. 2008), especially its inability to distinguish between areas of high and low use by the subject animal and its inclusion of too much unused space (Worton 1987, 1989). Nevertheless, it is still one of the most widely used methods of calculating home ranges (Powell 2000), largely because it is simple to construct and compare among studies (Harris *et al*. 1990). Furthermore, Boyle *et al*. (2009) showed that the MCP model can be more accurate than kernel models when the sample size is small, which is the case in our study. Home range areas based on the minimum convex polygon method have the advantage of being unaffected by possible autocorrelation between locations (Harris *et al*. 1990). Finally, given the extended periods without any sampling, the MCP model is the only one that could be applied to our data, as other models require stricter sampling regimes (Börger *et al*. 2006).

A home range is defined as “that area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt 1943). The key word in this definition is “normal”, i.e. a home range is not *all* the area that an animal traverses during a certain time, but rather the area where it *normally* moves. For this reason, most researchers delete outliers (often the 5% of locations contributing most to the area of a polygon around all locations) before home range estimation (White & Garrott 1990).

While 100% MCPs are more straightforward to compare, 95% MCPs (i.e. excluding 5% outliers) have been shown to be more exact representations of home ranges for the above reason, and are therefore preferred over 100% MCPs by many authors (e.g., Mazur *et al*. 1998, Bayne *et al*. 2001, Yaremych *et al*. 2004). In this study however, this approach would have been problematic: The night roosts of the Pampagrande & Pulquina clusters were the locations that added by far the most area to the respective seasonal home ranges and would thus be the first locations that have to be excluded to form 95% MCPs. However, we observed that macaws returned to the same night roosts regularly, a behaviour that is also reported by Pitter & Christiansen (1995). Thus, they must be considered integral parts of their seasonal home ranges, and excluding them would violate the very definition of a home range, i.e. that it

includes the animal's *normal* movements. Therefore I restricted myself to using 100% MCPs.

I used Hawth's Tools Extension to ArcGIS (Beyer 2004) to create a 100% MCP of all independent locations of a macaw as an estimate of its overall home range during our study period. I created 100% MCPs of each of the four above-mentioned clusters of locations as estimates of its seasonal home ranges.

I compared the 2008 and 2009 Pampagrande ranges. Because the 2009 seasonal home range in Pampagrande includes a distant night roost (some 29 km away from the centre of the MCP) that adds much area to the home range, whereas no such night roost was recorded in 2008, I excluded that night roost from the 2009 seasonal home range for comparison. Thus, the compared ranges can be considered seasonal feeding and daytime roosting areas (SFDRAs), which form part of a larger seasonal home range that would include night roosts.

The tests for spatial autocorrelation of the data and congruence of the Pampagrande 2008 and 2009 SFDRAs are based on Sokal & Sneeze (1963) and Hubert *et al*. (1981), and are similar to time-space-clustering of Mantel (1967). They use symmetric distance matrices that have zeros in their main diagonal.

To test for spatial autocorrelation of the data in each SFDRA, I created a distance matrix of all geographic data (x- and y-coordinates of locations) and another distance matrix of all temporal data (times of locations), each for the Pampagrande 2008 and 2009 data. For each season, I calculated the cophenetic correlation between the two distance matrices and then performed a randomization test of the approximation of 10.000 permutations of the cophenetic correlation between the distance matrices. This test for cophenetic correlation corresponds to the test for spatial autocorrelation. The cophenetic correlations are normal Pearson product-moment correlations.

To test for congruence of the 2008 and 2009 SFDRAs, I created one distance matrix of all geographic data (Pampagrande 2008 and 2009) and another distance matrix of the years. The latter is conceptually a design matrix containing only zeros (year differences within the 2008 and 2009 SFDRAs) and ones (year differences between the 2008 and 2009 SFDRAs). As in the autocorrelation test, I calculated the cophenetic correlation between the two

matrices and then performed a randomization test of the approximation of 10.000 permutations of the cophenetic correlation between the proximity matrices. In this case, a significant cophenetic correlation coefficient means that geographic distances within one SFDRA are significantly smaller than geographic distances between the SFDRAs (i.e. that the two SFDRAs are shifted against each other). The concept of this test is visualized in Fig. 4.

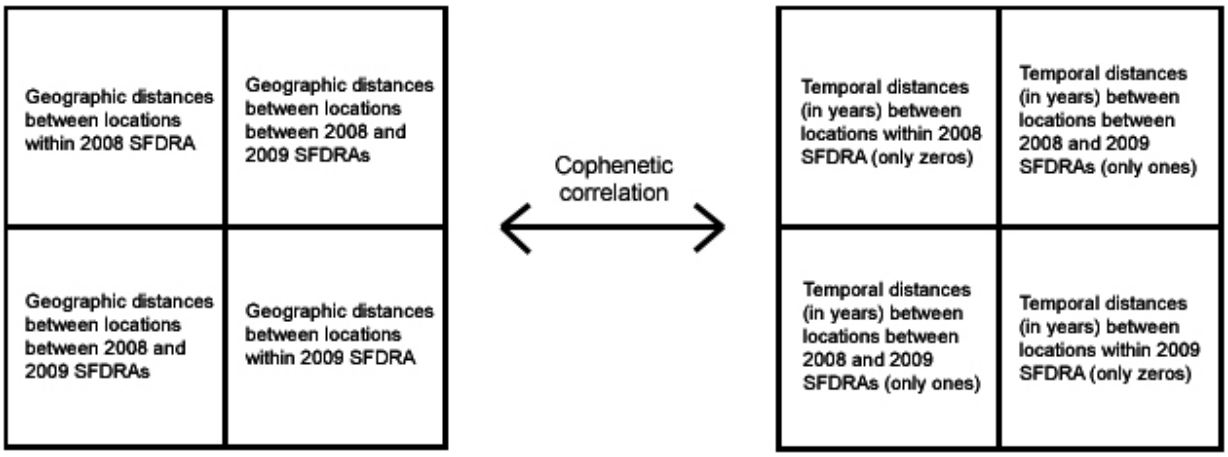


Fig. 4: Conceptual diagram of the cophenetic correlation analysis for congruence of the 2008 and 2009 Pampagrande SFDRAs. A distance matrix of all geographic distances between locations within and between the 2008 and 2009 SFDRAs is cophenetically correlated with a design matrix of differences between years within and between the 2008 and 2009 SFDRAs (only zeros and ones).

The 2008 SFDRA was larger than the 2009 SFDRA (see results), but this could theoretically be due to a few outliers. To test whether distances between 2008 locations are really larger than between 2009 locations (i.e. whether the SFDRA is larger), I compared mean distances between locations of the 2008 and 2009 distance matrices with a Welch's two sample t-test, the hypothesis being that mean 2008 distances are greater.

3.2.2. Sufficiency of the number of locations for reliable range estimates

For each range to be analysed, I randomly selected 3-20 locations (depending on the overall number of locations) and successively added further randomly selected locations, always measuring the area of an MCP around the selected locations. I then made incremental area plots (number of locations plotted against MCP area) to create observation-area curves in order to test for

asymptotic ranges (Odum & Kuenzler 1955). Adding randomly selected instead of successive locations is recommended by Harris *et al*. (1990) for discontinuous data.

3.2.3. Migration

Due to the obvious geographic and temporal distinction between the clusters, I subjectively determined the timing of possible migrations *a posteriori* (i.e. when an animal moved a long distance from one cluster/single point to another), rather than *a priori* defining criteria to establish endpoints of long-distance movements, which is usually necessary in migration studies (White & Garrot 1990).

4. Results

4.1. Baiting and trapping

The macaws were quite wary and it took several weeks of baiting before each of the successful capture attempts. After successful captures, macaws would avoid bait stations.

Five Red-fronted Macaws were captured on the morning of 25 August 2008. On 29 August 2008 several birds walked onto a baited trap and one bird was captured - however, unfortunately it turned out to be a recapture (macaw # 5). A further five macaws were captured on the morning of 22 July 2009, four of which were fitted with the remaining radio collars.

4.2. Measurements of radio-tagged birds

Table 1 shows body mass, morphometric data, and the presumed sex of the nine birds captured and equipped with radio collars. Based on the body mass values, one bird most certainly is a male, whereas the remaining eight birds probably are females. All nine birds were in adult plumage.

Macaw #	Mass (g)	Wing chord (cm)	Tail length (cm)	Tarsus length (mm)	Presumed sex [1]
1	540	28.9	30.1	27.3	Female
2	500	29.1	29.1	28.2	Female
3	510	28.6	30.0	24.3	Female
4	515	28.6	29.6 [2]	25.4	Female
5	615	28.7	30.2	25.6	Male
6	535	30.1	34.0	33.0	Female
7	530	30.0	32.5	32.7	Female
8	500	30.5	36.0	33.2	Female
9	500	30.0	29.0	33.3	Female

Table 1: Body mass, morphometric data and presumed sex of the nine Red-fronted Macaws equipped with radio collars on 25 August 2008 (macaws # 1-5) and 22 July 2009 (macaws # 6-9). [1] Based on body mass, males are heavier than females. [2] Tail ca. 1 cm broken off at tip.

4.3. Radio Tracking

The 17 months of field work resulted in 484 locations spread over 45 different days. After checking for autocorrelation of the different macaws, 193 independent locations of one macaw (# 4) remained for analyses (see below). Of these locations, 141 resulted from direct observations, 51 from triangulation, and one from the first overflight. During the second overflight, no signals were received. A Map of the searched area is shown in Fig. 5.

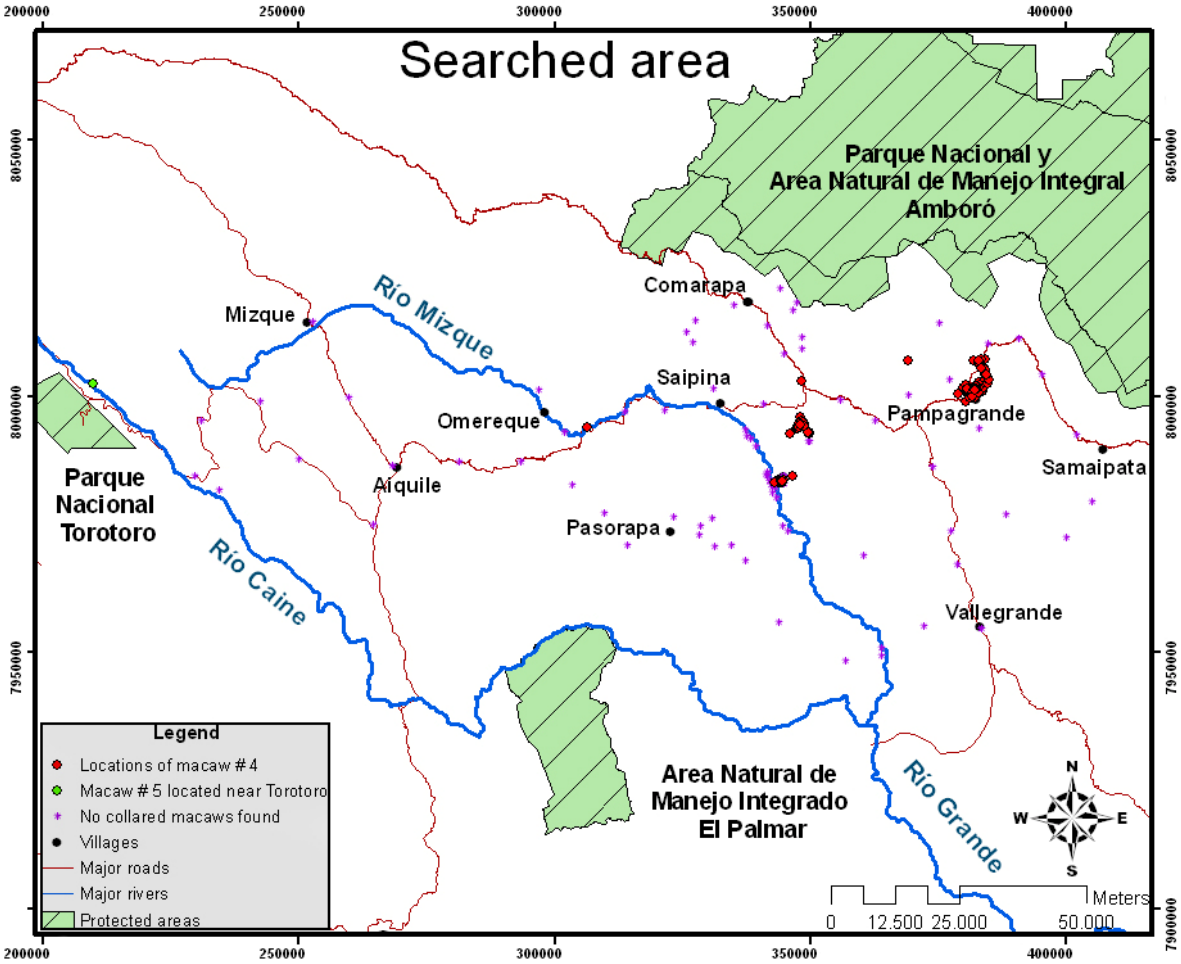


Fig. 5: Map of the searched area. Note the single location of macaw # 5 (green point) close to Parque Nacional Torotoro at the westernmost extreme of the species' range. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).

Although we recorded locations opportunistically without a strict sampling regime, in most areas we covered different time periods of the day more or less equally with our sampling (Appendix 1). The time between 10:15 and 14:15 is generally underrepresented in the Pampagrande ranges. This should not be a

big problem, as this time period falls within the midday rest when the macaws generally move little (Boussekey *et al*. 1991, Christiansen & Pitter 1997). In the Anamal area the sampling was less uniformly distributed over the different time periods, which indicates that the data might not be representative of the macaws' movements in that area.

4.4. Independence of the different macaws' locations

First analyses of the data showed that much of the locations were not mutually independent. In 60.3% of all cases (292 of 484), two or more macaws were recorded together at the same location. In these cases, each macaw's choice of where to move must not be interpreted as an individual, but as a group choice (D. Zinner, pers. comm.). Thus, the birds cannot be regarded as independent individual birds, but only as one group of birds (N = 1). Only the cases where only one radio-collared bird was located at a location can consequently be considered independent individual locations (IILs), while others must be considered group locations, and comparisons across individuals may only be made on the basis of IILs (Zinner, pers. comm.). An overview of overall locations, IILs, and group locations for the radio-collared macaws is given in Table 2.

Macaw #	**Overall locations**	**Independent individual locations (IILs)**		**Group locations**	
		No.	**%**	**No.**	**%**
1	55	4	7.3	51	92.7
2	56	2	3.6	54	96.4
3	47	5	10.6	42	89.4
4	194	126	64.9	68	35.1
5	90	24	26.7	66	73.3
6	11	10	90.1	1	9.9
7	12	10	83.3	2	6.7
8	10	7	70	3	30
9	9	5	55.6	4	45.4
Overall	**484**	**193**	**39.9**	**291**	**60.1**

Table 2: Number of overall locations, independent individual locations (IILs), and group locations for the nine radio-collared macaws.

Only two macaws yielded more than 10 IILs, # 4 (126 IILs) and # 5 (26 IILs). To test whether there are sufficient independent individual locations to use both # 4 and # 5 as independent birds in the analyses, I created 100% MCPs from IILs for # 4 and # 5 for each cluster, respectively. For each macaw and cluster I then compared the sizes of those 100% MCPs with 100% MCPs created from all locations. For macaw # 4, sizes of 100% MCPs were 43.0 ha compared to 100.7 ha (42.7%) in Anamal, 154.9 ha compared to 2,458.6 ha (6.3 %) in Pampagrande (2008), 5,731.9 ha compared to 5,737.6 ha (99.9%) in Pampagrande (2009), and 330.0 ha compared to 330.0 ha (100%) in Pulquina. For macaw # 5, sizes of 100% MCPs were 39.1 ha km² compared to 70.2 ha (55.7%) in Anamal and 193.6 ha compared to 2933.3 ha (6.6%) in Pampagrande (2008) (macaw # 5 was not located in the Pulquina area nor in Pampagrande in 2009). This means that if the two macaws were to be analyzed as individual birds, and consequently only IILs were to be used for analyses, in all but two cases (Pampagrande (2009) and Pulquina) the home ranges would be great underestimates.

In some instances signals of transmitters were received on neighbouring frequencies (i.e. they supposedly came from other transmitters). Tests with the equipment and observations in the field showed that those signals could only come from macaw # 4.

For the two above reasons, I decided to leave macaw # 5 out of further analyses and concentrate only on macaw # 4 (except for one especially remote independent location of macaw # 5 which will be discussed, see Fig. 5). Using only one bird for the analyses terminates the problem of individual choice versus group choice (as explained above), so I could include all locations of that bird, including the ones where two or more radio-collared birds were recorded together. This left me with a total of 194 independent locations, fixes of which were taken between 1228 meters and 1692 meters of elevation (locations of observer). A map of the independent locations of macaw # 4 is shown in Fig. 6.

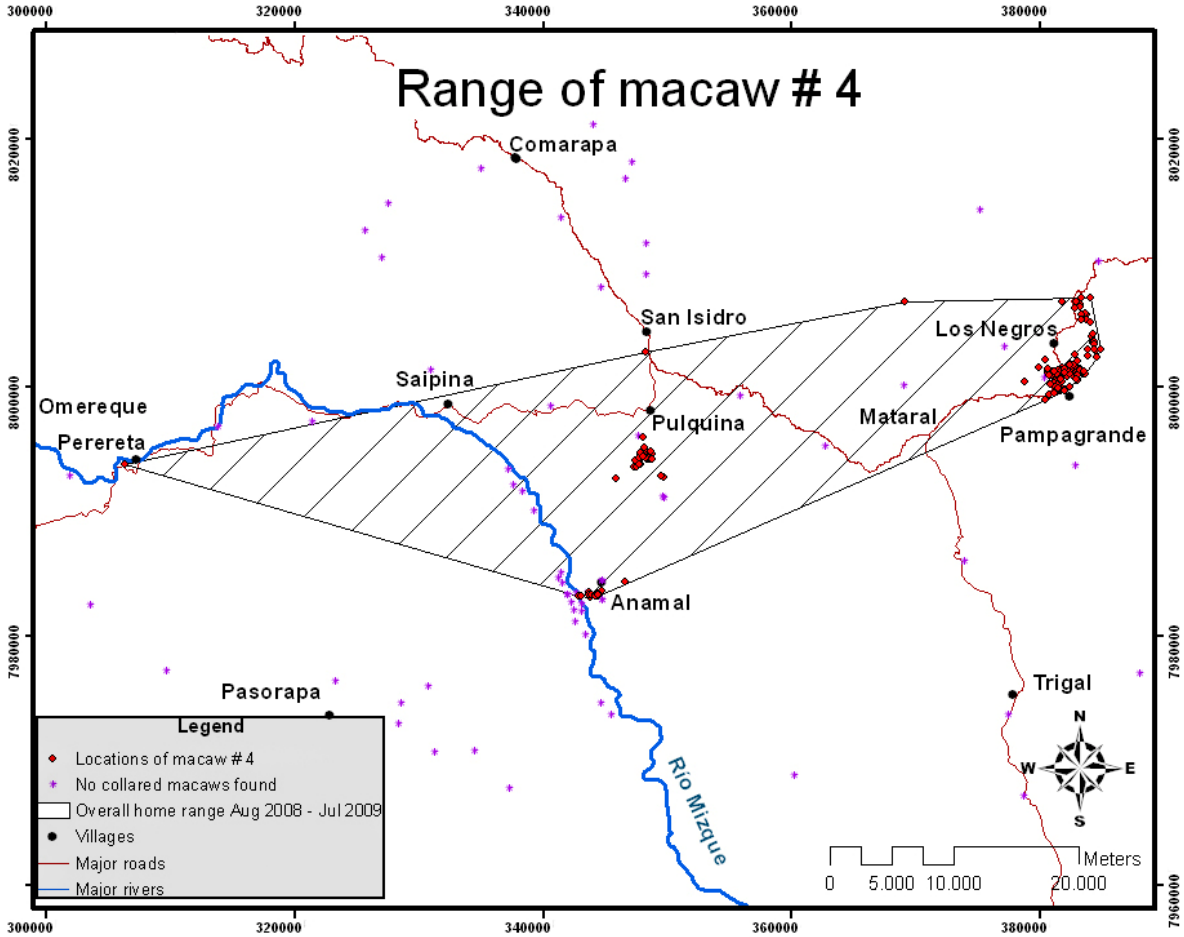


Fig. 6: Map of the supposed range of macaw # 4, inferred from its independent locations. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).

4.5. Home range estimation

Three to four of the MCPs were asymptotic (Pampagrande 2008, Pampagrande 2009, Pampagrande 2009 without night roost, and possibly Pulquina). Two of the MCPs were not asymptotic (Anamal and All locations Aug 2008 - Jul 2009). The observation-area curves for the different ranges are summarized in Appendix 2. Maps of the seasonal ranges are shown in Appendices 3 to 5.

Table 3 summarizes the 100% MCPs of macaw # 4 in the different seasonal ranges. The data from Anamal included neither triangulated locations nor direct-observation locations with observer-to-animal distances greater than 200 meters so no potential range of the estimate is given in this case.

Locality (Interpretation of MCP)	Size of 100 % MCP (ha)	Potential range of 100% MCP estimates (ha) under the consideration of estimation errors	No. of locations	Time of the year
Pampagrande 2008 (SFDRA)	2,458.6 *	2,198.3 - 2,722.7	57	25 Aug 2008 - 12 Dec 2008
Anamal (SHR)	100.7	-	19	4 Feb 2009 - 28 Feb 2009
Pulquina (SHR)	330 (*)	330 - 492.9	48	11 Apr 2009 - 30 Apr 2009
Pampagrande 2009 (SHR)	5,737.6 *	5,351.8 - 6,344.3	68	15 May 2009 - 29 July 2009
Pampagrande 2009 - w/o night roost (SFDRA)	1,465.3 *	1,213 - 1,901.2	67	15 May 2009 - 29 July 2009
All localitions Aug 2008 - Jul 2009 (OHR)	90,428	-	194	25 Aug 2008 - 29 July 2009

Table 3: Range estimates of macaw # 4. Codes in brackets are interpretations of MCPs: SFDRA = seasonal feeding and daytime roosting area, SHR = seasonal home range, OHR = overall home range Aug 2008 - Jul 2009. Asterisks indicate asymptotic MCPs and reliable estimates.

4.6. Vegetation types in the seasonal home ranges

The vegetation in the Pampagrande seasonal home ranges was a mixture of inter-Andean dry forest and Tucuman-Bolivian forest and was characterized by phreophytic trees like *Prosopis alba*, *Celtis tala*, and *Schinopsis haenkeana* as well as the cactus *Samaipaticereus corroanus*. The night roost of the 2009 Pampagrande seasonal home range as well as Anamal and Pulquina seasonal home ranges lay in inter-Andean semi-dry forest with dominant *Schinopsis haenkeana* and *Neocardenasia herzogiana*. Especially the Pampagrande and Pulquina areas also contained anthropogenic plant communities on crop fields, pastures and fallows and deforested zones (Navarro & Maldonado 2002).

4.7. Comparison of the 2008 and 2009 seasonal feeding and daytime roosting areas (SDFRAs) in Pampagrande

In the tests for spatial autocorrelation in the 2008 data, the empirical cophenetic correlation coefficient (r-value) of the cophenetic correlation between the two distance matrices was 0.02. Of the 10,000 correlation coefficients gained from random permutations 3,309 (33.09%) were larger than the empirical cophenetic correlation coefficient. The explained variance (r^2) is <0.001, i.e. less than 0.1% of the variance can be explained by autocorrelation. Therefore, in the 2008 data there is no significant autocorrelation (N=56, *p*=0.33, r=0.02, SD=0.07, z=0.36).

In the tests for spatial autocorrelation in the 2009 data, the empirical cophenetic correlation coefficient of the cophenetic correlation between the two distance matrices was 0.09. Of the 10,000 correlation coefficients gained from random permutations 698 (6.98%) were larger than the respective empirical cophenetic correlation coefficient. The explained variance is <0.01. Therefore, in the 2009 data there is a near-significant autocorrelation (N=68, *p*=0.07, r=0.09, SD=0.06, z=1.60). Because of the high *N* and accordingly, the high statistical power of the test, even the relatively small autocorrelation of 0.09 was near-significant, but this small autocorrelation can be neglected.

Because of the very low explained variance in both cases, autocorrelation is not of concern for the following tests which assume the data to be independent.

In the test for range congruence, the empirical cophenetic correlation coefficient between the two distance matrices was 0.05. Only 48 (0.48%) of the 10,000 correlation coefficients gained from random permutations were larger than the empirical cophenetic correlation coefficient. The explained variance was <0.003. Therefore, there was a highly significant cophenetic correlation between the two distance matrices and therefore a shift of the SFDRAs between the years (N=124, *p*<0.01, r=0.05, SD=0.01, z=4.25). The shift, measured as the distance between the centres of the SFDRAs, was 939.6 meters.

The Welch's two sample t-test for differences in mean distances between locations of the 2008 and 2009 SFDRAs showed that mean 2008 distances were significantly greater than mean distances between 2009 locations (p-value <0.01). Therefore, the hypothesis that the 2008 SFDRA was greater than the

2009 SFDRA cannot be rejected. The mean distance was 2629.4 meters in 2008 and 2421.0 meters in 2009 (Fig. 7).

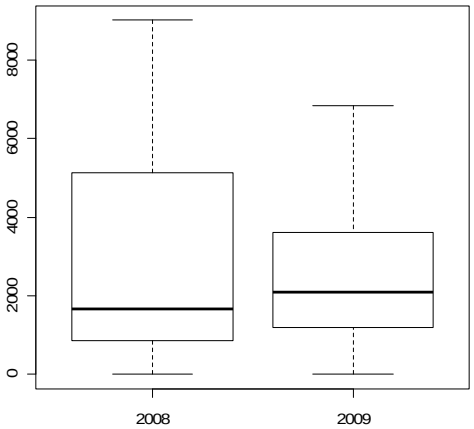


Fig. 7: Box plot of distances between random locations within the 2008 and 2009 SFDRAs, respectively. Note that although the median distance between locations is greater in 2009 (solid horizontal line in the box), mean distances between locations are significantly greater in 2008.

4.8. Night roosts

On one evening in the Pampagrande area, we managed to follow macaw # 4 up to a communal night roost 13.48 km away from the centre of that seasonal range. During some of the following mornings and evenings, signals were received from that night roost, too. Its position was congruent with indications by locals and our own observations as to the direction in which macaws left in the evening.

In the Pulquina area the bird would come from and leave towards the same direction every morning and evening, respectively. We managed to follow macaw # 4 to a communal night roost 2.87 km from the centre of that seasonal range.

Each night roost was visited by more than 60 macaws. They were located in narrow valleys which contained neither roads nor cultivations but high forest. Several groups of macaws would arrive from the feeding grounds in the evening and first gather in trees on the upper slopes of the valleys. They would successively fly further down to the lower slopes of the valleys where they would roost in high trees. In the morning, first vocalizations started during early dawn and the macaws left well before sunrise from 6:00 am onwards.

4.9. Minimum daily covered distances

We managed to record locations hourly on four days, all during April 2009 in the Pulquina area. For the estimation of minimum daily covered distances I assumed that the bird spent every night at the same respective night roost (see above). Under this assumption, the mean minimum daily covered distance during the four days in April was 9.01 kilometres (SD=0.82). In Pampagrande I measured 28.5 kilometres as a minimum daily covered distance (not based on hourly fixes). Minimum daily covered distances are summarized in table 4. A map showing the daily flight routes in the Pulquina area which were the basis for covered distance calculations is shown in Appendix 6.

Date	Locality	Minimum daily covered distance (km)	Number of locations upon which the estimate is based
12.04.2009	Pulquina	8.48	11
13.04.2009	Pulquina	9.50	11
19.04.2009	Pulquina	8.17	11
20.04.2009	Pulquina	9.89	9
mean	Pulquina	9.01 (SD=0.82)	10.5
21.05.2009	Pampagrande	28.5	4

Table 4: Minimum daily covered distances for four days in April 2009 in Pulquina and one day in May 2009 in Pampagrande.

4.10. Migration

From the day of its capture (25 August 2008) macaw # 4 stayed in the Pampagrande area until at least 21 December 2008, then moved west across the San Isidro area (24 December) and by 14 January 2009 it had reached its westernmost recorded locality, Perereta, some 77 kilometres west of Pampagrande. By 4 February 2009 it had moved to the Anamal area, some 40 kilometres from Perereta, where it stayed at least until 26 February. On 11 April 2009 it was first discovered in the Pulquina area, some 12 kilometres from Anamal, where it stayed at least until 30 April. By 15 May it had reached the Pampagrande area, some 45 kilometres from Pulquina, again, where it stayed until its last location was recorded on 20 July 2009 (Fig.8).

Macaw # 5 covered a distance of at least 170.6 kilometres between the point where it had been captured (Pampagrande) and the point where it was located during the first overflight (Torotoro) (Fig. 5).

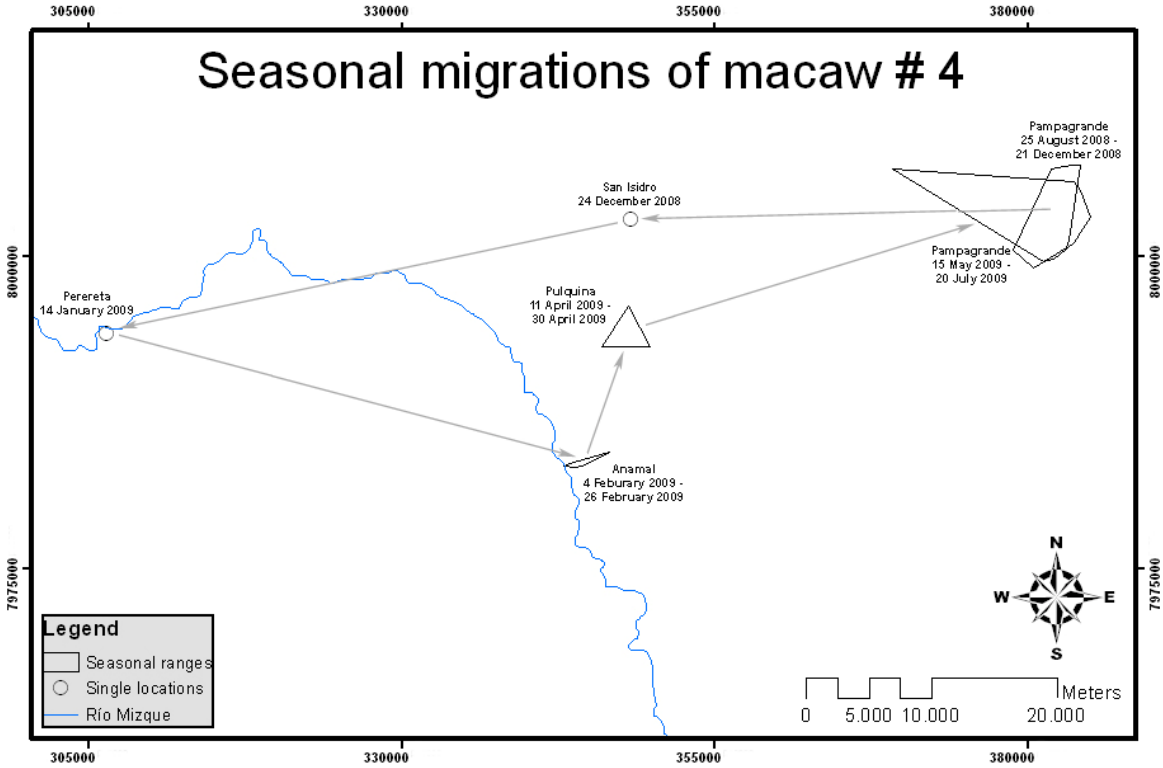


Fig. 8: Seasonal migrations of macaw # 4. Grey arrows denote the direction of migrations.

4.11. Flock sizes

On several occasions in Pampagrande, I observed flocks of more than 100 Red-fronted Macaws, while the maximum number of macaws counted in a single flock was 214 (counted from photographs, see Appendix 7).

5. Discussion

5.1. Discussion of the results of the telemetry study

5.1.1. Spatial ecology of the Red-fronted Macaw

5.1.1.1. Radio telemetry

Previous studies have successfully employed radio telemetry to study the ecology of psittacines (Lindsey *et al*., 1991, Lindsey *et al*., 1994, Snyder *et al*., 1994, Meyers, 1996, Meyers *et al*., 1996, Robinet *et al*. 2003, Ndithia & Perrin 2006, Stahala 2008), including Buffon's Macaws in northeastern Costa Rica (Bjork & Powell 1995, Monge *et al*. 2003), Scarlet Macaws in central Pacific Costa Rica (Marineros & Vaughan 1995, Myers & Vaughan 2004), and Hyacinth Macaws in the Brazilian Pantanal (Antas *et al*. 2006).

With only 489 locations over a 17 months period in our study, we had a comparably lower success rate than other studies, which is due to several complicating aspects of the field work.

Financial restrictions kept us from using a 4x4 vehicle during much of the time, which would have been necessary to access more remote parts of the study region. Also, for budget reasons, the team was only able to undertake two overflights, while ideally the team would have been able to overfly the area until every individual was found whenever there hadn't been a signal for a predefined period (White & Garrott 1990).

Due to social and political unrest during the first three weeks of September 2008 in Santa Cruz department all overland roads were blocked, making travel to the study area impossible, and no field work was conducted during this period.

Finally, even during the times we spent searching the area by car, the success in locating the macaws was limited. There are several possible explanations for this.

As the terrain is very rugged, with deep canyons and high hills, reception of the signals was probably hindered by geographic obstacles in many instances. Because of the little-developed road system, much of the area remained

inaccessible to us. Even in areas where there were roads, these were often in poor condition, so that it was rarely possible to cover large distances in a short time, which is one of the reasons why we frequently lost the macaws' trace while trying to follow them. For logistic reasons, it was not possible to search much of the Río Caine area, nor the Río Pilcomayo. It is therefore possible that most radio-tacked macaws spent much of the 17 months either in parts of their range where we did not search or in hidden valleys that we could not reach.

The fact that macaw # 4 was found somewhat regularly over the study period and that no macaws were found during a second overflight makes their absence from the Río Mizque area or transmitter failure more likely than simply not having detected them despite their presence and functioning transmitters.

Although the transmitters are parrot-proof according to Hololil Systems, published evidence that radio-collars really withstand the strong parrot bills is restricted to other radio-collars manufactured by North Star (Myers 1996, Myers & Vaughan 2004), and there are anecdotal notes of macaws biting through thin iron bars (Santa Cruz Zoo, pers. comm.). Therefore, we cannot rule out the possibility that the macaws destroyed the brazen collars during social preening. Radio transmitter failure, even without the parrots destroying the transmitters themselves, is a frequently reported problem (White & Garrott 1990). Finally, a further reason for not finding some of the macaws could be that they died or were captured.

5.1.1.2. Triangulation

The accuracy test for the triangulation data showed a large mean deviation (550.56 meters) of the estimated from the actual location, compared to other such studies (e.g., Sierro *et al*. 2001, Carillo *et al*. 2002, Keurighlian *et al*. 2004). The obvious trend that several clusters of locations are separated by larger areas without any locations was not weakened by the inclusion of most triangulation data, even when the estimation error was considered. The sizes of the seasonal home ranges did differ considerably when the estimation error was considered, but their definite sizes are of relatively little conservation relevance compared to the broader implications of the trend that small clusters of locations are spread over a large area, which will be discussed below.

5.1.1.3. Home ranges

The overall home range of 90,428 hectares cannot be considered a reliable estimate. The home range size is not asymptotic, and I expect the true home range to be larger towards its western edge, as there are extended periods without any received signals from the time when the macaw was in that area, suggesting that it had roamed further to areas which we could not reach. On the other hand, MCPs often overestimate the home ranges because they contain large areas of unoccupied space if home ranges do not have a convex shape (Worton 1987, 1989, Powell 2000).

Macaw # 4 spent extended periods in different seasonal home ranges. Their combined area of 6,909 hectares is small compared to the overall area it roamed during the course of the year.

Despite being asymptotic, the size of the Pampagrande 2008 MCP (2,459 ha) cannot be regarded as a reliable estimate of the macaws' seasonal home range as it does not include night roosts, which are an integral part of a home range and are often somewhat distant to the feeding grounds. Instead, it can be interpreted as a seasonal feeding and daytime roosting area. The true Pampagrande 2008 seasonal home range will likely be greater. The asymptotic Pampagrande 2009 MCP (5,738 ha) can be interpreted as a seasonal home range. It could be an underestimate, as we cannot be certain that macaw # 4 only used one night roost during that period (see below). The Pulquina MCP (330 ha) might be an underestimate of the seasonal home range as it is not clearly asymptotic. The Anamal MCP (101 ha) is not asymptotic nor does it include night roosts, and is therefore probably an underestimate of the seasonal home range.

The significant incongruence and difference in size of the 2008 and 2009 Pampagrande seasonal feeding and daytime roosting areas (2,459 ha and 1,465 ha, respectively) are not straightforward to interpret. Changing ecological factors in the course of the year might be an explanation as sampling took place at different times of the year (25 Aug 2008 - 12 Dec 2008 and 15 May 2009 - 29 July 2009, respectively), but it is equally likely that the differences are the result of different durations of the sampling periods (109 days and 75 days,

respectively). Finally, a sampling bias (i.e. the 2008 team systematically searched at different sites than the 2009 team) might also play a role.

It is difficult to decide whether to consider the seasonal home range established by the macaw in the Anamal area as a breeding or wintering home range. The bird was recorded in the area for a period of just over three weeks (although it could have stayed there longer), but breeding by Red-fronted Macaws is recorded for the high cliffs in the area and the time of the year (February) lies within the breeding period (Ridgely 1981). Apparently, macaw # 4 did not breed in the 2008/09 breeding season (although it possibly tried to establish a breeding territory in Perereta or Anamal). This is not surprising as not all adults seem to breed every year and the number of adults in the vicinity of the few well-studied breeding cliffs is 21-45 % greater than the number of breeding pairs (S. Herzog, pers. comm.).

The seasonal home ranges established in Pampagrande and Pulquina on the other hand can be considered wintering home ranges, as no breeding cliffs are found in nearby areas and despite the last locations of the 2008 Pampagrande seasonal home range falling in the breeding season (November to March) according to the literature.

The sizes of these wintering home ranges (between 330 and 5,738 ha) cannot be compared to the estimated breeding season home range size of 5,000 ha given by Pitter & Christiansen (1995) as it refers to a population and not individuals and the underlying method of home range estimation was not made clear by the authors.

Home ranges reported for other macaw species are 247 ha in Green-winged Macaws and 1,326 ha in Blue-and-yellow Macaws in south-western Peru (Brightsmith & Boyd 2009), 31,720 ha in Hyacinth Macaws in the Pantanal (Antas *et al*. 2006), 56,000 ha in Scarlet Macaws in central pacific Costa Rica (Marineros & Vaughan 1995), and 418,300 ha in Lear's Macaws in eastern Brazil (IBAMA 2006).

5.1.1.4. Night roosts

Earlier studies which only concentrated on the breeding season reported that Red-fronted Macaws roost in cliffs that they also use for nesting, and only very

rarely in trees (Clarke & Duran-Patiño 1991, Pitter & Christiansen 1995). Contrary to this, the night roosts found in our study during the wintering season consisted of narrow and steep valleys with high forest where the macaw would roost in trees on the lower slopes of the valleys. The tendency to gather at sleeping roosts is common behaviour among parrots (Chapman *et al*. 1989).

Lear's Macaw, another endangered macaw species endemic to an arid ecosystem, is also reported to usually roost in cliffs (Yamashita 1987) but also trees (Araújo 1996).

The night roosts found in our study were 2.9 km and 13.5 km from the respective feeding grounds. Pitter and Christiansen (1995) found roost sites between 6 km and 15 km from the respective feeding areas. For Lear's Macaws, distances between night roosts and feeding areas range from 12-32 km (Brandt & Machado 1990) to 80 km (Rigueira & Sherer Neto 1997).

On some occasions in 2009 we located macaw # 4 close to Pampagrande very early in the morning, suggesting that it also used other (i.e. closer) night roosts. Using different night roosts has been reported for Rosy-faced Lovebirds (Ndithia & Perrin 2009).

5.1.1.5. Minimum daily covered distances

The minimum daily covered distances are closely related to the distance between the night roost and the feeding area. Hourly fixes in Pulquina (9-11 fixes a day), where the feeding area is 2.9 km from the night roost, resulted in a mean minimum daily covered distance of 9.0 kilometres, whereas in the Pampagrande area (13.5 km from night roost) the minimum covered distance estimated from just four fixes was 28.5 kilometres.

Araújo (1996) estimated possible movements between roosting and different feeding areas of 24.9 – 169.5 km per day for Lear's Macaws.

5.1.1.6. Migration and site fidelity

Migration is defined by White and Garrott (1990) as a regular, roundtrip movement of individuals between two or more areas or seasonal ranges, as opposed to dispersal which they define as a one-way movement of individuals

from their natal site or an area that has been occupied for a period of time. Furthermore, they define fidelity as the tendency of an animal to return to an area previously occupied or to remain in one defined area for an extended period of time.

Little is known about migration in macaws. Several studies on different macaw species (e.g., Syvitski 1998, Bjork & Powell 1994, Matola & Sho 2002) have investigated movement patterns in general or migration in particular, but few of those studies (e.g., Antas *et al*. 2006) resulted in publications in peer-reviewed journals. The Red-fronted Macaw was considered resident by Lanning (1982) and Pitter and Christiansen (1995).

Macaw # 4 stayed in the main wintering area near Pampagrande until the middle of December 2008, which is unusually late, compared to other years, when most macaws had moved away until the beginning of the austral summer in early to mid-November (S. Herzog, pers. comm.). The macaw was located in the largest breeding colony at Perereta in January 2009 and later in a minor breeding area in Anamal in February 2009. By mid-May 2009 it had reached the Pampagrande wintering grounds again.

The data available in this study so far only covers one year, so no conclusions can be made as to the regularity of the movement pattern of macaw # 4. The macaw did, however, undertake a roundtrip movement between different areas, at least three of which were occupied for an extended period of time and can qualify as seasonal ranges, and thus showed a marked migration pattern.

Furthermore, macaw # 4 showed strong winter site fidelity in that particular year, because after leaving the Pampagrande area in mid-December 2008 and travelling at least some 77 kilometres away from Pampagrande, it returned to the same area between early and mid-May 2009. Observations in the Pampagrande area of more than one hundred Red-fronted Macaws year after year (S. Herzog, pers. comm.) and at least 214 during our field work support the hypothesis that this site fidelity is typical for a relatively large part of the global population of the species.

Reasons for site fidelity to Pampagrande would likely be linked to food sources. The timing of the largest aggregations of Red-fronted Macaws in Pampagrande coincided with the peanut and maize harvesting periods, respectively, and the

macaws were regularly seen feeding on the crops, usually in the morning and late afternoon.

Over the last years in Perereta, Armonía scientists witnessed the successive leaving of most breeding macaws after the nesting season, while only very few seem to stay year-round. Therefore, I believe that Red-fronted Macaws usually migrate away from their nesting areas to different feeding grounds for wintering. This is consistent with statements by local inhabitants that the macaws move over large areas in search of maize (Boussekey *et al*. 1991), but contrary to Pitter and Christiansen (1995), who believed that the species is resident and makes only short excursions to maize fields close to their breeding cliffs.

Observations from other parts of their range agree with reports by local farmers that several areas with large peanut or corn fields are visited by large flocks of macaws during the respective harvesting periods, which further supports the hypothesis that the species migrates in response to shifting seasonal feeding opportunities, taking particular advantage of cultivated crops.

It is also possible that the population studied by Pitter and Christiansen in the lower Río Caine valley does in fact not migrate, because that area boasts both large breeding cliffs and nearby peanut and maize fields (Pitter & Christiansen 1995, A. Rojas, pers. comm.). It has also been shown for Mealy Parrots that parts of a population migrate while others do not (Bjork 2004), so it is not possible to conclude on movements of the whole population from observations of just a few radio-collared birds.

It is also difficult to draw conclusions on the degree of migratory behaviour and site fidelity of the species prior to the creation of large peanut and maize fields in the area as there is virtually no literature on the species from that time.

Seasonal migrations in response to shifting feeding opportunities are common among macaws (Bjork & Powell 1994, 1995, Bonadie & Bacon 2000, Matola & Sho 2002, Karubian *et al*. 2005, Contreras-Gonzalez *et al*. 2009), and also other psittacines are known to track food resource availability (Pizo *et al*. 1995, Renton 2001, 2002, Symes & Perrin 2003, Bjork 2004). Most similarly to Red-fronted Macaws, Military Macaws in Mexican dry forests also breed in cliffs and undertake seasonal movements to more distant feeding grounds after the breeding season (Salazar 2001, Bonilla-Ruz *et al*. 2007).

The strong site fidelity for the wintering grounds near Pampagrande contrasts with a study on Swift Parrots, another endangered and migrant parrots species which also inhabits dry habitat but is much more nomadic in its wintering grounds than the Red-fronted Macaw (Mac Nally & Horrocks 2000). In contrast to the macaws wintering in Pampagrande, this species uses highly scattered and unpredictable food sources during wintering. As peanuts and maize are highly nutritive food sources that are clumped and fairly predictable, site fidelity to these feeding grounds in Red-fronted Macaws is not surprising.

One macaw showing marked migration pattern and winter site fidelity out of nine radio-tagged birds cannot provide any statistical proof that this behaviour is typical for the species. Nor can the fact that migration and site fidelity could not be documented for eight out of nine macaws provide any prove for the contrary, as other factors than absence from the area are equally likely explanations for their non-detection (see above). The above argumentation does, however, suggest that macaw # 4 showed a ranging behaviour that is typical for at least part of the global population of Red-fronted Macaws. A satellite or GPS tracking study could clarify this question (see below). Both seasonal migrations and site fidelity have also been suggested for Spix's Macaws (Juniper & Yamashita 1991).

5.1.2. Flock sizes

Flock sizes seem to be larger during the wintering period than during the nesting season. I regularly observed flocks of more than 100 birds and counted a maximum number of 214 macaws in a single flock, which far exceeds published breeding season flock sizes of up to 90 (Pitter & Christiansen 1995).

5.1.3. Implications of this study for conservation and future research

5.1.3.1. General movement patterns

Red-fronted Macaws seasonally occupy rather small home ranges, in which they breed (nesting season) or exploit highly clumped food sources such as peanut and maize fields (wintering season). At least some of these seasonal

home ranges are used regularly by a large part of the global population. Maintaining the macaw-friendly character of such key sites (e.g., Pampagrande, Perereta) will likely be of great value for the conservation of the species.

On the other hand, Red-fronted Macaws seem to move widely between seasonal home ranges in the course of a year, so both local sites and the landscape will have to be considered in conservation planning for the species.

5.1.3.2. Connectivity between subpopulations

An important factor for the survival of the species is whether or not the small global population is divided into genetically isolated subpopulations. The fact that a male (# 5) that was captured near the eastern extreme (Pampagrande) was located during the overflight some 170 km away near the western extreme (Torotoro) of the species' range, suggests that at least some individuals move widely through the species range (at least the northern part of it), providing sufficient connectivity for genetic exchange. Whether or not there is any connectivity between the Caine/Mizque and the Pilcomayo subpopulations remains unclear.

5.1.3.3. Telemetry

Based on our experience with radio telemetry on Red-fronted Macaws, it appears reasonable to say that radio-tracking failed to yield most of the desired results, because of a combination of difficult terrain, political instability as well as logistic and financial constraints. It also seems likely that most of these constraints (especially the terrain aspect) cannot be overcome in the near future. I would therefore consider radio telemetry not to be an effective means of studying Red-fronted Macaws in the wild.

Other authors have reported similar difficulties in studying parrot populations, especially macaws, with radio telemetry. They recommend for future studies improved capacity to track animals, including simultaneous monitoring by multiple researchers and periodic searches from aircraft (Myers & Vaughan

2004). An easier, more reliable, and possibly cheaper way might be the use of satellite or GPS telemetry.

The constant and assured influx of higher quality data that would have been possible through the use of satellite transmitters or GPS-RF tags would have allowed for more sophisticated analyses, including more accurate home range estimates, as well as statistical validation of the results. Accurate home range estimates are important for the understanding of a species' spatial ecology (Powell 2000), as well as for the implementation of conservation and management programs (Clemmons & Buchholz 1997, Caro 1998).

A major constraint to satellite/GPS tracking is the high cost of satellite transmitters and GPS-RF tags, and many radio tracking users feel the costs are prohibitively high (White & Garrott 1990). However, Harrington *et al*. (1987) present economic data indicating that satellite transmitters can be more cost effective than conventional radio transmitters in some cases. Another obvious constraint to satellite/GPS tracking many bird species is the weight of the transmitters (Fiedler 2009).

A proposal by Armonía for PTT (Platform Transmitting Terminals) satellite transmitters was rejected because the bird:PTT weight ratio was considered too close, resulting in two much risk for the instrumented individuals.

Recent technological advances have enabled scientists to satellite/GPS track birds of a similar size or even smaller than Red-fronted Macaws. These studies include satellite tracking of Eastern Bar-tailed Godwits (Gill *et al*. 2008), Eurasian Hobbies (Fiuczynski *et al*. 2009), and Eleonora's Falcons (Lopez-Lopez *et al*. 2009) as well as GPS-tracking of Oilbirds (Holland *et al*. 2009) and Trumpeter Hornbills (J. Lenz, pers. comm.). Macaw-proof PPT units have been tested successfully on the larger Scarlet (WCS-Guatemala & CEMEC 2007) as well as Green-winged and Yellow-and-blue Macaws (Brightsmith & Boyd 2006, 2009). This gives hope that much-needed satellite/GPS telemetry studies can be conducted on Red-fronted Macaws in the future as well.

The amount of information that could be drawn from our data was greatly compromised by autocorrelation between the different macaws, which is why I could only analyse data of one macaw eventually, in spite of the considerable amount of money and time that has been invested in the study of nine macaws. Despite the obvious difficulty of catching macaws, I therefore strongly

recommend that not the first captured macaws be fitted with transmitters, but that during each successful capture only one macaw is selected, and, if possible, that different birds be captured at different locations. These measures would maximize the possibility of independence of movements among the macaws and therefore increase the overall efficiency of the study, despite the larger effort to capture macaws. This is generally recommended for telemetry studies (White & Garrott 1990).

Variability between the sex and/or age classes can be expected for movement parameters, and given the small overall sample size that can likely be achieved because of the high cost of transmitters, I recommend considering to instrument only one sex-age class (e.g. adult females) in the future.

5.2. Discussion of published and unpublished literature on the conservation of Red-fronted Macaws

5.2.1. Threats

Like all larger birds with a relatively small range, the Red-fronted Macaw is predisposed for extinction (Bennett & Owens 1997, Gage *et al*. 2004). However, while most authors regard habitat degradation as the biggest threat to the species, there are conflicting perceptions regarding both the status of the species and the severity of other threats such as trapping, direct persecution, and disturbance, amongst others.

5.2.1.1. Habitat degradation and Red-fronted Macaws as a crop pest

Several authors argue that the macaws feed on agricultural crops because of shortages of natural food sources resulting from man-made habitat alterations. They claim that as the semi-deciduous forests along the rivers which were the species' natural feeding areas are increasingly being destroyed for agriculture, the species has to resort on agricultural crops, especially in the non-breeding season (Pitter & Christiansen 1995, Brace *et al*. 1995).

Different species of parrots and macaws have been reported to cause damage to crops during periods of low natural fruit availability (e.g. Long 1985, Bucher 1992, Bonadie & Bacon 2000), most notably Lear's Macaw, which like the Red-fronted is an endangered endemic of a dry habitat, and feeds heavily on maize as a result of the destruction of their primary feeding habitat, Licuri palm stands (Brandt & Machado 1990, IBAMA 2006). However, Lear's Macaws depend heavily on Llicuri palm fruits year-round, and stands have been reduced to an estimated 1.6% of their original cover (IBAMA 2006). Therefore, a causal relationship between habitat loss and feeding on crops is much more apparent than in the case of Red-fronted Macaws.

During the non-breeding season we regularly observed the macaws feeding on peanut and maize crops even in areas with abundant fruiting "Soto" (*Schinopsis haenkeana*), which is one of the most important natural food plants at that time of the year and readily fed on by the birds during mid-day roosting. One should consider that a ripe peanut or corn field probably provides a much higher mass of available energy per unit area than a natural forest, and the soft shells of peanuts and maize probably require less handling time per unit mass of obtained nutrients than the hard seeds of most local trees (although I did not quantify this), which would make crops an attractive food source, rather than a last resort. Pitter and Christiansen (1995) themselves acknowledged that the macaws "greatly preferred maize, even when it was in short supply and a wide choice of abundant native fruit existed". Captive macaws of several species also show this preference (Abramson 1995). Therefore, rather than a necessity because of the scarcity of natural fruit plants, their feeding on crops could equally be interpreted as an opportunistic behavioural adaptation to a new resource, resulting in the observed large aggregations on the agricultural feeding grounds during winter. This argumentation is supported by village elders in Pampagrande, who claim that in the 1970s when agricultural fields were still fewer and smaller, there were no such large winter aggregations of Red-fronted Macaws in the area, and neither were they a problem as a crop pest (A. Langer, pers. comm.). Blue-and-yellow Macaws in the Brazilian Cerrado have also been shown to use recent anthropogenic landscape elements opportunistically (Tubelis 2009).

5.2.1.2. Factors limiting the abundance of Red-fronted Macaws

Despite my doubts regarding a causal relationship between shortages of natural food plants and the macaws' feeding on cultivated crops, I do not question the macaws' dependence on natural food plants and the associated threats from deforestation throughout the species' range per se. Macaws generally have a narrow diet and typically only use between 10 % and 23 % of available food resources (Contreras-González *et al*. 2009 and references therein), which makes them vulnerable to changes in food resource availability associated with habitat alterations (Saunders 1977, Renton 2006). Peanuts and maize are not available throughout much of the year, so Red-fronted Macaws continue to depend on natural forests with large trees for feeding, as well for roosting and perching. The loss of semi-deciduous forests in the valleys could therefore well be a limiting factor for the macaws' abundance. The authors of the two more extensive studies on Red-fronted Macaws (Clarke & Duran-Patiño 1991, Pitter & Christiansen 1995) believe that loss of their primary habitat (estimated at 40 % in 1991) is the biggest threat for the species.

It is equally possible, however, that Red-fronted Macaws (being strong flyers able to move over large areas) can track sufficient resources in the fragmented landscape even though a large percentage of the original habitat is destroyed. The ability to use small forest remnants in fragmented landscapes has been shown for Blue-winged Macaws (Conti Nunes & Galetti 2007) as well as some other psittacines (Fischer & Lindenmayer 2002, MacNally & Horrocks 2000, Marsden *et al*. 2000).

Trapping is another important threat for many parrot species (Collar & Juniper 1992, Snyder *et al*. 2000) and was regarded as the key threat for Red-fronted Macaws during the 1970s and early 1980s (Ridgely 1981, Lanning 1982). The problem was since then considered less severe than habitat loss because the species has been afforded more legal protection (Lanning 1991, Boussekey *et al*. 1991, Clarke & Duran-Patiño 1991, Pitter & Christiansen 1995). Yet, recent work indicating that trapping continues (A. Rojas, pers. comm.) and that in fact large numbers of Red-fronted Macaws are still traded illegally every year (Herrera & Hennessey 2007) makes it equally possible that trapping is the most important limiting factor for population recovery.

Another limiting factor that is reported for many other psittacines is nesting opportunities. In many macaw species, major problems lie in failures to lay eggs or in poor success of egg-laying pairs (Snyder *et al*. 2000). During our field work we spoke with several locals who claimed that nearby cliffs had been used for nesting by macaws in the past, but not so anymore. A possible explanation for that could be increased human disturbance near the nest sites. Clarke and Duran Patiño (1991) stated that Red-fronted Macaws apparently favour those cliffs free of human disturbance, based on local accounts from Perereta. On the other hand, we observed breeding macaws in Perereta paying little attention to human disturbance. Christiansen & Pitter (1993b) report the same from a tributary of the Rio Grande and do not believe suitable nest holes to be la limiting factor.

Despite these discrepancies regarding the importance of different threats, no one has as yet tried to quantify their relative impact on the population. It is unlikely that all threats can be efficiently tackled at the same time. Given the general scarcity of financial resources in conservation programmes, efforts should be made to tackle threats in a most efficient manner (i.e. give priority to threats that have the largest effect on the population).

Clarke & Duran-Patiño (1991) argue that “however interesting further biological information would be, we believe that we must concentrate on research directed at saving the species (setting up protected areas) and that biological study of the species must wait.” I disagree with that statement. Although reserves can play an important role in parrot conservation (e.g. Marsden *et al*. 2000, Stahala 2008), and the creation of an adequate reserve system in the inter-Andean dry forests would certainly benefit many endemic species (Larrea-Alcazar & López 2005, López & Zambrana-Torrelio 2005), there is as yet no assurance that the establishment of reserves will be the most effective management option for the recovery of Red-fronted Macaw populations. Parrot declines are commonly correlated with habitat deterioration, but one should not simply assume that this proves a primary cause and effect relationship without further supporting data (Snyder *et al*. 2000).

Mistaken assumptions about the causes of population decline can be the worst enemy of conservation programmes, and failure in conservation management efforts often traces to lack of sufficient information about basic natural history

features of the species in question and incorrect identification of main causes of endangerment (Caughley 1994, Snyder *et al*. 2000).

A famous example of unscientific risk analysis, the California Condor programme was long compromised by the assumption that habitat loss was the major threat and millions of US$ were spent on habitat preservation, which however did not halt the species' decline. It was only through radio-telemetry-aided demographic studies that lead poisoning was finally identified as the most important cause of decline (Snyder & Snyder 1989).

Main limiting factors of population growth can be established via quantitative evaluations of both reproduction and mortality (Snyder *et al*. 2000, Dunning *et al*. 2006). The adoption of demographic modelling and especially sensitivity analysis has been a key conservation development (Caughley 1994, Finkelstein *et al*. 2010). The various forms of sensitivity analysis (e.g., Crouse *et al*. 1987, Wisdom *et al*. 2000, Caswell 2001, Morris & Doak 2002, Baxter *et al*. 2006) can identify key life stages or demographic processes (e.g. survival, growth, reproduction) as management targets and quantitatively tie alternative management actions to population persistence. They have been widely used to justify and prioritize management plans for different bird species (e.g., Lande 1988, Anderson & Mahato 1995, Drechsler *et al*. 1998, Katzner *et al*. 2006, Whitfield *et al*. 2006, Finkelstein *et al*. 2010).

As such models are very sensitive to the quality of the data and the use of poor-quality demographic data can seriously impair decisions in bird conservation (Reed *et al*. 1998, Beissinger & Westphal 1998), a long-term demographic study on Red-fronted Macaws should be carefully designed and strictly implemented (Snyder *et al*. 2000). The importance of establishing demographic parameters for Red-fronted Macaws is also highlighted by Kyle (2005). Such a study could disentangle the relative importance of different mechanisms of population regulation (e.g., food shortage, trapping, lack of nesting opportunities, etc.) for the species, and eventually enable managers to set up a robust and more effective conservation plan for the species.

5.2.2. Status of the Red-fronted Macaw

There are large discrepancies between the different status estimates, from below 1000 (Clarke & Duran Patiño 1991) to 3000-5000 (Lanning 1982, 1991). However, most of these estimates are based on extrapolations from relatively small sampled areas and should be viewed with caution. A further problem of most of the estimates is that the birds were usually considered to be resident (Lanning 1982, Pitter & Christiansen 1995), which is probably not the case (see above).

As pointed out by Clarke and Duran Patiño (1991), estimates of abundance based on observations of birds away from their habitual roosting/breeding sites are bound to be unreliable, because for wide-ranging species one cannot know whether birds observed in one area are distinct from birds observed in another, especially if the different areas are also surveyed at different times of the year.

This problem can be demonstrated by a report of Herzog *et al*. (1997): they found only one Red-fronted Macaw during five days spent in an area of the Rio Caine valley in June 1991, where 40 birds were encountered by one of the authors in Oct./Nov. 1989, 60 birds had been estimated to be present in Oct./Nov. 1990 by Boussekey *et al*. (1991), and ca. 100 from Sept. 1991 to March 1992 by Pitter and Christiansen (1995). Likewise, I counted more than 200 Red-fronted Macaws in a single flock in Pampagrande in June 2009, where just two months before we only found a dozen or so.

To counter this problem, Clarke and Duran Patiño (1991) restricted their survey to the nesting period and to known and proposed nesting areas (mostly large cliffs along rivers) along the Rio Grande and Rio Mizque valleys and extrapolated their findings only for a total of 269 km that they considered possible breeding areas along those river systems.

As Clarke and Duran Patiño, Pitter and Christiansen (1995) carried out a survey during the breeding periods and predominantly along river valleys with adjacent large cliffs (i.e. suitable for nesting). But contrary to them they extrapolated their findings not only for all similarly suitable nesting areas, but also for all areas that they considered suitable feeding areas (evergreen valleys as well as valleys with farmland) in the macaws' presumed range. This is problematic, as prime nesting areas are expected to hold much higher

concentrations of macaws than other feeding areas during the breeding season, whereas feeding areas away from the breeding areas could be virtually devoid of macaws at that time of the year.

I therefore believe the smaller estimate of Clarke and Duran Patiño to be more reliable. Taking into account that they did not consider the other large river systems of the area, Caine and Pilcomayo, their results are surprisingly similar to estimates from the extensive counts of active and potential nests (700-800, including a conservative estimate of 264-579 reproducing individuals), carried out by Armonía in recent years (S. Herzog, pers. comm.).

This leads to the question of trends in the macaws' population. If one only considers the relatively large numbers estimated by the majority of the earlier studies, the much lower numbers estimated in the last few years would suggest a dramatic population decline and possibly warrant a reclassification of the species' conservation status to 'Critically Endangered'. If, on the other hand, one trusts the estimate of Clarke and Duran Patiño, the population could be considered very small but relatively stable over the last 20 years. As the two scenarios could imply different conservation options, there is an obvious need for continuous and methodologically constant monitoring of population trends of this highly endangered species.

5.3. Conclusions

1. Radio-telemetry has not been a very effective tool to study the spatial ecology of Red-fronted Macaws in the wild and is unlikely to be very successful in the future. Other methods such as satellite or GPS tracking should be considered.
2. The species is not strictly resident as has been claimed by earlier authors, at least a large part of the global population is most probably migrant.
3. Red-fronted Macaws seem to move widely in the course of a year, but show strong site fidelity to relatively small areas seasonally. While maintaining the macaw-friendly character of such key sites will benefit the species, the landscape aspect will also have to be considered in conservation planning for the species. At least in the northern parts of the species' range, population connectivity is unlikely to be of great concern for this potentially wide-ranging species.
4. Still, hardly anything is known about the southern part of the species' range (Río Pilcomayo), and research in that area should be a priority.
5. Recommendations for management and conservation of the species given by earlier authors are in part based on unwarranted assumptions and need to be treated with caution. The relative importance of different threats as factors limiting population recovery has not been quantified to date.
6. Demographic studies, following strict sampling regimes, are recommended to allow robust decisions in the future conservation management of Red-fronted Macaws.
7. As past population estimates cannot be considered reliable, it is imperative to implement a monitoring program, also following a strict and constant sampling regime, to establish whether or not the population is in decline and to follow future population developments.

References

Abramson, J., 1995. Nutritional Requirements. Pages 111-145 *in*: Abramson, J., Speer, B.L., & Thomson, J.B. (eds.). The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Fort Bragg, California, USA.

Anderson, M.C. & Mahato, D., 1995. Demographic models and reserve designs for the California Spotted Owl. Ecological Applications 5:639-647.

Antas, P.T.Z., Carrara, L.A., Yabe, R.S., 2006. Radio tracking adult Hyacinth Macaws in the Pantanal, central Brazil. Meeting Information: 24th International Ornithological Congress Hamburg, Germany. Journal of Ornithology Volume: 147:Suppl. 1:128-129.

Antezana, C. & Navarro, G., 2002. Contribución al análisis biogeográfico y catálogo preliminar de la flora de los valles secos interandinos del centro de Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 12:3-38.

Araújo, J.C.C., 1996. Relatório Técnico Parcial das Atividades de Campo (novembro de 1995 a abril de 1996) – Programa de Conservação e Manejo da Arara-Azul-de-Lear (*Anodorhynchus leari*). Fundação Biodiversitas, 1996.

Bayne, E.M., Hobson, K.A., 2001. Movement patterns of adult male ovenbirds during the post-fledging period in fragmented forested boreal landscapes. Condor 103:343-351.

Baxter, P.W.J., McCarthy, M.A., Possingham, H.P., Menkhorst, P.W. & McLean, N., 2006. Accounting for management costs in sensitivity analyses of matrix population models. Conservation Biology 20:893–905.

Beissinger, S.R., Brice, A. & Wiley, J., 1994. Recommendations from the APC on Scarlet Macaw conservation in Costa Rica. Unpublished report. Association for Parrot Conservation, Arlington, VA, USA.

Beissinger, S.R. & Westphal, S.I., 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Bennett, P.M. & Owens, I.P.F. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society of London Biological Series 264:401-408.

Berger, D.D. & Mueller, H.C., 1959. The Bal-chatri trap: a trap for the birds of prey. Journal of Field Ornithology 30:18-26.

Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. Available at www.spatialecology.com/htools.

Bianchi, C.A., 1998. Biología reproductiva da Araracaninde (*Ara ararauna*, Psittacidae) no Parque Nacional das Emas, Goiás. M.S. thesis. Departamento de Ecologia, Universidade de Brasília, Brasília-DF, Brazil.

BirdLife International, 2008. *Ara rubrogenys*. *In*: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. Downloaded from www.iucnredlist.org on 22/8/2010.

BirdLife International, 2009. Important Bird Area factsheet: Cuencas de Ríos Caine y Mizque, Bolivia. Downloaded from the Data Zone at www.birdlife.org on 1/9/2010.

BirdLife International, 2010. Species factsheet: *Ara rubrogenys*. Downloaded from www.birdlife.org on 6/7/2010.

Bjork, R. & Powell, G.V.N., 1994. Intratropical migration by *Ara ambigua*: identifying habitat heterogeneity to protect biodiversity in lowland tropical wet forest of Central America. Unpublished report to the Wildlife Conservation Society.

Bjork, R., Powell, G.V.N., 1995. Buffon's Macaw: some observations on the Costa Rican population, its lowland forest habitat and conservation. Pages 387-392 *in*: Abramson, J., Speer, B., Thomsen, J. (eds.). The Large Macaws: Their Care Breeding and Conservation. Raintree Publications, Fort Bragg, California, USA.

Bjork, R., 2004. Delineating pattern and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning. PhD Thesis, Oregon State University, Corvallis, OR, USA.

Bonadie, W.A. & Bacon., P.R., 2000. Year-round utilization of fragmented palm swamp forest by Red-bellied Macaw (*Ara manilata*) and Orangewinged Parrots (*Amazona amazonica*) in the Nariva Swamp (Trinidad). Biological Conservation 95:1-5.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A. Lovari, S. Coulson, T., 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393-1405.

Boulanger, J.G., & White, G.C., 1990. A comparison of home-range estimators using Monte Carlo simulation. Journal of Wildlife Management 54:310-315.

Boussekey, M., Saint-Pie, J., & Morvan, 0., 1991. Observations on a population of Red-fronted Macaws *Ara rubrogenys* in the Río Caine valley, central Bolivia. Bird Conservation International 1: 335-350.

Boyle, S.A., Lourenco, W.C., da Silva, L.R., & Smith, A.T., 2009. Home range estimates vary with sample size and methods. Folia Primatologica 80:33-42.

Brace, R.C., Hesse, A.J., & White, A.G., 1995. The endemic macaws of Bolivia. Cotinga 3:27-30.

Brandt, A., Machado, R.B., 1990. Área de alimentação e comportamento alimentar de *Anodorhynchus leari*. Ararajuba, 1:57-63.

Brightsmith, D., & Boyd, J., 2006. Testing satellite telemetry tags for psittacines in Tambopata, Peru. A report to Loro Parque Foundation, North Star Science and Technology, Amigos de las Aves, USA, Parrot Conservation Research Fund.

Brightsmith, D. & Boyd, J., 2009. Large macaw satellite telemetry in Tambopata, Peru. Progress as of October 2009. Available at http://filesdown.esecure.co.uk/wildlifepark/Satellite_telemetry_Progress_Oct_09_3_.pdf_20102009-0944-53.pdf

Brightsmith, D. & Bravo, A., 2006. Ecology and management of nesting Blue-and-yellow Macaws (*Ara ararauna*) in Mauritia palm swamps. Biodiversity and Conservation 15:4271-4287.

Brown, D.R., Stouffer, P.C., Strong, C.M., 2000. Movement and territoriality of wintering Hermit Thrushes in southeastern Louisiana. Wilson Bulletin 112:347-353.

Bucher, E.H., 1992. Neotropical parrots as agricultural pests. Pages 201-220 *in*: Beissinger, S.R., Snyder, N.F. (eds.). New World Parrots in Crisis. Smithsonian Institution Press, Washington, D.C, USA.

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Caccamise, D.F., Hedin, R.S., 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97:306-318.

Calvo. B., Furness, R.W., 1992. A review of the use and the effects of marks and devices on birds. Ringing and Migration 13:129-151.

Caro, T., 1998. The significance of behavioral ecology for conservation biology. Pages 3-26 *in*: Caro, T. (ed.). Behavioral Ecology and Conservation Biology. Oxford University Press, New York, New York, USA.

Caughley, G., 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Chapman, C.A., Chapman, L.J., Lefebvre, L., 1989. Variability in parrot flock size – possible functions of communal roosts. Condor 91:842-847.

Christiansen, M.B. & Pitter, E. 1993a. Aspects of behaviour of juvenile Red-fronted Macaws, *Ara rubrogenys*, in the wild. Gerfaut 83:63-69.

Christiansen, M.B., & Pitter, E., 1993b. Aspects of breeding behaviour of Red-fronted Macaws, Ara *rubrogenys*, in the wild. Gerfaut 83:51-61.

Clarke, R.O.S. & Duran-Patiño, E., 1991. The Red-fronted Macaw *Ara rubrogenys* in Bolivia: distribution, abundance, biology and conservation. Unpublished report to the International Council for Bird Preservation.

Clemmons, J.R., Buchholz, R., 1997. Linking conservation and behavior. Pages 3-22 *in*: Clemmons, J.R., Buchholz, R. (eds.). Behavioral Approaches to Conservation in the Wild. Cambridge University Press, Cambridge, UK.

Collar, N.J. & Juniper, A.T., 1992. Dimensions and causes of the parrot conservation crisis. Pages 1-24 *in*: Beissinger, S.R. & Snyder, N.F.R. (eds.). New World Parrots in Crisis: Solutions from Conservation Biology. Smithsonian Institute Press, Washington, DC, USA.

Collar, N.J., Crosby, M.J. & Stattersfield, A.J. 1994. Birds to Watch 2: The World List of Threatened Birds. BirdLife International, Cambridge, UK.

Collar, N. J., 2000. Globally threatened parrots: criteria, characteristics and cures. International Zoo Yearbook. 37:21-35.

Conti Nunes, M.F., Galetti, M., 2007. Use of forest fragments by blue-winged macaws (*Primolius maracana*) within a fragmented landscape. Biodiversity and Conservation Volume: 16:953-967.

Contreras-Gonzalez, A.M., Rivera-Ortiz, E.A., Soberanes-Gonzalez, C., et al., 2009. Feeding ecology of Military Macaws (*Ara miltaris*) in a semi-arid region of central Mexico. Wilson Journal of Ornithology 121:384-391.

Crouse, D.T., Crowder, L.B. & Caswell, H., 1987. A stagebased population-model for Loggerhead Sea-turtles and implications for conservation. Ecology 68:1412-1423.

del Hoyo, J., Elliott, A., Sargatal, J., 1997. Handbook of the Birds of the World, Sandgrouse to Cuckoos. Lynx Editions, Barcelona, Spain.

Drechsler, M., Burgman, M. & Menkhorst, P., 1998. Uncertainty in population dynamics and its consequences for the management of the Orange-bellied Parrot *Neophema chrysogaster*. Biological 84:269-281.

Dunning, J.B., Groom, M.J., & Pulliam, H.R., 2006. Species and Landscape Approaches to Conservation. Pages 419-465 *in*: Groom, M.J., Meffe, G.K., Carroll, C.R. (eds.). Principles of Conservation Biology, 3rd ed. Sinauer, Sunderland, MA, USA.

Eckert, R., Randall, D., 1988. Animal physiology: mechanisms and adaptations. W. H. Freeman, New York, New York, USA.

Embert, D., 2002. Reptilien der Provinz Florida/ Bolivien. Ökologie, Systematik und Verbreitung. 2002. Unpublished diploma thesis, Rheinische Friedrichs-Wilhelm Universität, Bonn.

ESRI, 2005. ArcGIS 9.2. Environmental Systems Research Institute Inc., Redlands, CA, USA.

Fiedler, W., 2009. New technologies for monitoring bird migration and behaviour. Ringing & Migration 24:175.179.

Finkelstein, M.E., Doak, D.F., Nakagawa, M., Sievert, P.R., & Klavitter, J., 2010. Assessment of demographic risk factors and management priorities: impacts on juveniles substantially affect population viability of a long-lived seabird. Animal Conservation 13: 148-156

Fischer, J., Lindenmayer, D.B., 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. Biodiversity Conservation 11:833-849.

Fiuczynski, K.D., Howey, P.W., Meyburg, C., & Meyburg, B.-U., 2009. Intercontinental migration of an Eurasian Hobby (*Falco subbuteo*) tracked by means of a 5g satellite transmitter. 7th Conference of the European Ornithologists' Union 2009, University of Zurich, Switzerland (Poster).

Forshaw, J.M., 1989. Parrots of the World, 3rd ed. Lansdowne, Willoughby, Australia.

Fuller, K.S. & Gaski, A., 1987. Update to Latin American wildlife trade laws. World Wildlife Fund. Washington, DC, USA.

Gage, G.S., Brooke, M. de L., Symonds, M.R.E., & Wege, D., 2004. Ecological correlates of the threat of extinction in neotropical bird species. Animal Conservation 7:161-168.

Gill, R.E. Jr, Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T., 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proceedings of the Royal Society B 276:447–457.

Gonzáles, L. & Reichle, S., 2003. Reptilos. Pages 137-140 *in*: Ibisch P.L. & Mérida, G., (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Harrington, F.H., Veitch, A.N., & Luttich. S.N., 1987. Tracking barren-ground and woodland caribou by satellite: the more the need for PPTs, the better they work. Pages 221-242 *in*: Proceedings of the Argos Users Conference. Service Argos, Greenbelt, MD, USA.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T., & Wray, S., 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97-123.

Herzog, S.K., 2003. Aves. Pages 141-145 *in*: Ibisch P.L. & Mérida, G., (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Herzog, S.K., Kessler, M., Maijer, S., & Hohnwald, S., 1997. Distributional notes on birds of Andean dry forests in Bolivia. Bulletin of the British Ornithological Club 117:223-235.

Herrera, M. & Hennessey, B., 2007. Quantifying the illegal parrot trade in Santa Cruz de la Sierra, Bolivia with emphasis on threatened species. Bird Conservation International 17:295-300.

Holland, R.A., Wikelski, M., Kümmeth, F., Bosque, C., 2009. The secret life of Oilbirds: new insights into the movement ecology of a unique avian frugivore. PLoS ONE 4(12): e8264. doi:10.1371/journal.pone.0008264

Hubert, L.J., Golledge, R.G., & Costanzo, C.M., 1981. Generalized procedures for evaluating spatial autocorrelation. Geographical Analysis 13:225.

Hupp, J.W., Ratti, J.T., 1983. A test of radiotelemetry triangulation accuracy in heterogeneous environments. Proceedings of the International Wildlife Biotelemetry Conference 4:31-46.

IBAMA, 2006. Management plan for the Lear's Macaw (*Anodorhynchus leari*). Brazilian Institute of Environment and Natural Renewable Resources, Fauna Species Protection Coordination. Ibama Editions, Brasília-DF, Brazil.

Ibisch, P.L., Beck, S.G., Gerkmann, B., & Carretero, A., 2003a. Ecoregiones y ecosistemas. Pages 47-88 *in*: Ibisch, P.L. & Mérida, G. (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Ibisch, P.L., ChiveCarretero, A., Beck, S.G., Cúellar, S., Espinoza, S., Araujo, N.V., 2003b. El caso de los bosques andinos. Pages 272-284 *in*: Ibisch P.L. & Mérida, G., (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Ibisch, P.L., Chive, J.C., Espinoza, S.D., & Araujo, N.V., 2003c. Hacia un mapa del estado de conservación de los ecosistemas de Bolivia. Pages 264-271 *in*: Ibisch P.L. & Mérida, G., (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

IUCN, 2010. IUCN Red List of Threatened Species. Version 2010.2. Downloaded from www.iucnredlist.org on 22/8/2010.

Juniper. T., Parr, M., 1998. Parrots: a guide to the parrots of the world. Pica Press, London, England.

Juniper, A.T. & Yamashita, C., 1991. The habitat and status of Spix's Macaw *Cyanopsitta spixii*. Bird Conservation International 1:1-9.

Karubian, J., Fabarra, J., Yunes, D., Jorgenson, J.P., Romo, D., & Smith. T.B., 2005. Seasonal and spatial variation in macaw abundance in the Ecuadorian Amazon. Condor 107:617-626.

Katzner, T.E., Bragin, E.A., & Milner-Gulland, E.J., 2006. Modelling populations of long-lived birds of prey for conservation: A study of imperial eagles (*Aquila heliaca*) in Kazakhstan. Biological Conservation 132:322-335.

Keuroghlian, A., Eaton, D.P., Longland, W.S., 2004. Area use by White-lipped and Collared Peccaries (*Tacassu pecari* and *Tapassu tajacu*) in a tropical forest fragment. Biological Conservation 120:411-425.

Kyle, T., 2005. Mountain macaws: an expedition to survey the breeding cliffs of Bolivia's Red-fronts. *Psittascene* 17.3:4-7.

Lande, R., 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia 75:601-607.

Lanning, D. 1982. Survey of the Red-fronted Macaw *Ara rubrogenys* and Caninde Macaw *Ara caninde* in Bolivia, December 1981 - March 1982. Unpublished report to the New York Zoological Society and International Council for Bird Preservation.

Lanning, D., 1991. Distribution and breeding biology of the Red-fronted Macaw. Wilson Bulletin 103:357-365.

Larrea-Alcazar, D. & López, R.P., 2005. An estimation of the floristic richness of Bolivia's Andean dry valleys. Biodiversity and Conservation 14:1923-1927.

Lindsey, G.D., Arendt, W.J., Kalina, J., Pendelton, G.W., 1991. Home range and movements of juvenile Puerto Rican Parrots. Journal of Wildlife Management 55:318-322.

Lindsey, G.D., Arendt, W.J., Kalina, J., 1994. Survival and causes of mortality in juvenile Puerto Rican Parrots. Journal of Field Ornithology 65:76-82.

Long, J., 1985. Damage to cultivated fruit by parrots in the south of Western Australia. Australian Wildlife Research 12:75-80.

López, R.P., 2003. Diversidad y endemismo de los valles secos bolivianos. Ecología en Bolivia 38:28-60.

López, R.P., Zambrana-Torrelio, C., 2005. Representation of Andean dry ecoregions in the protected areas of Bolivia: the situation in relation to the new phytogeographical findings. Biodiversity and Conservation 15:2163-2175.

Lopez-Lopez, P., Liminana, R., Urios, V., 2009. Autumn migration of Eleonora's Falcon *Falco eleonorae* tracked by satellite telemetry. Zoological Studies 48:485-491.

MacNally, R.M., Horrocks, G., 2000. Landscape-scale conservation of an endangered migrant: the Swift Parrot (*Lathamus dicolor*) in its winter range. Biological Conservation 92:335-343.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220.

Marineros, L. & Vaughan, C., 1995. Scarlet Macaws of Carara. Pages 445-467 *in*: Abramson, J., Speer, B., & Thomsen, J. (eds.). The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Fort Bragg, California, USA.

Marsden, S.J., Whiffin, M., Sadgrove, L., & Guimarães, P.R., 2000. Parrot populations and habitat use in and around two lowland Atlantic forest reserves, Brazil. Biological Conservation 96:209-217.

Matola, S. & Sho, E., 2002. Field Investigations of the Belize Scarlet Macaw (*Ara macao cyanoptera*). Ministry of Natural Resources, Belmopan, Belize.

Mazur, K.M., Frith, S.D., James, P.C., 1998. Barred Owl home range and habitat selection in the boreal forest of central Saskatchewan. Auk 115:746-754.

Meyers, J.M., 1996. Evaluation of 3 radio transmitters and collar designs for *Amazona*. Wildlife Society Bulletin 24:15-20.

Meyers, J.M., Arendt, W.J., & Lindsey, G.D., 1996. Survival of radiocollared nestling Puerto Rican parrots. Wilson Bulletin 108:159-163.

Mildenstein, T.L., Stier, S.C., Nuevo-Diego, C.E., et al., 2005. Habitat selection of endangered and endemic large flying-foxes in Subic Bay, Philippines. Biological Conservation 126:93-102.

Miyaki, C., Ribeiro de Oliveira-Marques, A., 2006. Molecular phylogeny and characterization of the mitochondrial DNA control region of the genera *Ara* and *Primolius* (macaws and allies, Psittaciformes). 24th International Ornithological Congress Hamburg, Germany. Journal of Ornithology 147:Suppl. 1: 212.

Montes de Oca, I., 1982. Geografía y recursos naturales de Bolivia. Academia Nacional de Ciencias de Bolivia, La Paz, Bolivia.

Morris, W.H. & Doak, D.F., 2002. Quantative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc., Sunderland, USA.

Munn, C.A., 1992. Macaw biology and ecotourism, or when a bird in the bush is worth two in the hand. Pages 47-72 *in*: Beissinger, S.R. & Snyder, N.F.R. (eds.). New World Parrots in Crisis. Smithsonian Institution Press, Washington, D.C., USA.

Munn, C.A., 1995. Lears Macaw: a second population confirmed. PsittaScene7:1-3.

Muñoz-Reyes, J., 1980. Geografia de Bolivia. 2nd ed. Academia National de Ciencias de Bolivia, La Paz, Bolivia.

Myers, M.C. & Vaughan, C., 2004. Movement and behavior of Scarlet Macaws (*Ara macao*) during the post-fledging dependence period: implications for in situ versus ex situ management. Biological Conservation 118:411-420.

Naef-Daenzer, B., 1993. A new transmitter for small animals and enhanced methods of home-range analysis. Journal of Wildlife Management 57:680-689.

Ndithia, H., Perrin, M.R., 2006. The spatial ecology of the Rosy-faced Lovebird *Agapornis roseicollis* in Namibia. Ostrich 77:52-57.

Nilsen, E.B., Pedersen, S., & Linnell, J.D.C., 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635-639.

Nycander, E., Blanco, D.H., Holle, K.M., Campo, A., Munn, C.A., Moscoso, J.I., & Ricalde, D.G., 1995. Manu and Tambopata: nesting success and techniques for increasing reproduction in wild macaws of southeastern Peru. Pages 423-443 *in*: Abramson, J.,

Spear, B.L., & Thomsen, J.B. (eds.). The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Fort Bragg, CA, USA.

Pimley, E.R., Bearder, S.K., & Dixson, A.F., 2005. Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. International Journal of Primatology 26:191-205.

Pitter, E. & Christiansen. M.B., 1995. Ecology, status and conservation of the Red-fronted Macaw *Ara rubrogenys*. Bird Conservation International 5:61-78.

Pitter, E. & Christiansen, M.B., 1997. Behavior of individuals and social interactions of the Red-fronted Macaw *Ara rubrogenys* in the wild during the mid-day rest. Ornitología Neotropical 8:133-143.

Pizo, M.A., Simao, I, & Galetti, M., 1995. Diet and flock size of sympatric parrots in the Atlantic Forest of Brazil. Ornitología Neotropical 6:87-95.

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. Pages 65-110 *in*: Boitani, L. & Fuller, T.K. (eds.). Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, USA.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reed, J.M., Murphy, D.D., & Brussard, P.F., 1998. Efficacy of population viability analysis. Wildlife Society Bulletin 26:244-251.

Renton, K., 2001. Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. Condor 103:62–69.

Renton, K., 2006. Diet of adult and nestling Scarlet Macaws in southwest Belize, Central America. Biotropica 38:280–283.

Ridgely, R.S., 1981. The current distribution of mainland neotropical parrots. Pages 233-284 *in*: Pasquier, R.F. (ed.). Conservation of New World Parrots. Smithsonian Institution Press / International Council for Bird Preservation. Washington, D.C., USA.

Rigueira, S. & Scherer-Neto, P, 1997. Arara-azul-pequena *Anodorhynchus leari*: Plano de ação para a sua conservação. Ibama, 1997.

Robinet, O., Bretagnolle, V., Clout, M., 2003. Activity patterns, bahitat use, foraging behaviour and food selection of the Ouvea Parakeet (*Eunymphicus cornutus uvaeensis*). Emu 103:71-80.

Salazar, T.J.M., 2001. Registro de la guacamaya verde (*Ara militaris*) en los cañones del Río Sabino y Río Seco, Santa María Tecomavaca, Oaxaca, México. Huitzil 2:18–20.

Salazar-Bravo, J. & L. Emmons, L., 2003. Pages 146-148 *in*: Ibisch, P.L. & Mérida, G., (eds.). Biodiversidad: La Riqueza de Bolivia. Estado de Conocimiento y Conservación. Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Saunders, D.A., 1977. The effect of agricultural clearing on the breeding success of the White-tailed Black Cockatoo. Emu 77:180-184.

Seaman, D.E., Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Shaprio, S.S. & Wilk, M.B., 1965. An analysis of variance test for normality (for complete samples). Biometrika, 52:591-611.

Sierro, A., Arlettaz, R., Naef-Daenzer, B., et al., 2001. Habitat use and foraging ecology of the Nightjar (*Caprimulgus europaeus*) in the Swiss Alps: Towards a conservation scheme. Biological Conservation 98:325-331.

Snyder, N.F.R., Koenig, S.E., Koschman, J., Snyder, H.A., & Johnson, T.B., 1994. Thick-billed Parrot releases in Arizona. Condor 96:845-862.

Snyder, N.F.R., McGowan, P., Gilardi, J., & Grajal, A. (eds.). 2000. Parrots. Status Survey and Conservation Action Plan 2000–2004. IUCN, Gland, Switzerland and Cambridge, UK.

Snyder, N.F.R. & Snyder, H.A. 1989. Biology and conservation of the California Condor. Pages 175-263 *in*: Power, D.M. (ed.). Current Ornithology: Volume 6. Book News, Inc., Portland, OR, USA.

Sokal, R.R. & Sneath, P.H.A., 1963. Principles of numerical taxonomy. W.H. Freeman and Co., San Francisco, CA, USA.

Springer, J.T., 1979. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management 43:926-935.

Stahala, C., 2008. Seasonal movements of the Bahama Parrot (*Amazona leucocephala bahamensis*) between pine and hardwood forests: Implications for habitat conservation. Ornitologia Neotropical 19:165-171.

Symes, C.T. & Perrin, M.R., 2003. Seasonal occurrence and local movements of the Grey-headed (Brown-necked) Parrot *Poicephalus fuscicollis suahelicus* in southern Africa. African Journal of Ecology 41:299–305.

Syvitski, C., 1998. Migration routes of the Hyacinth Macaw. *In*: 12th Conference on Animal Things, 4-9 February, Jura, Scotland.

Tubelis, D.P., 2009. Feeding ecology of *Ara ararauna* (Aves, Psittacidae) at firebreaks in western Cerrado, Brazil. Biotemas 22:105-115.

USGS/Glovis. Landsat Satellite Images are downloadable via U.S. Geological Survey/Global Visualisation Viewer at http://glovis.usgs.gov/.

Vaughan, C., 2002. Conservation strategies for a Scarlet Macaw (*Ara macao*) population in Costa Rica. Ph.D. Dissertation, University of Wisconsin, Madison, WI, USA.

Vaughan, C., Nemeth, N., Cary, J. & Temple, S., 2005. Response of a Scarlet Macaw (*Ara macao*) population to conservation practices in Costa Rica. Bird Conservation International 15:119-130.

WCS-Guatemala & CEMEC 2007. Testing satellite telemetry tags for psittacines in Petén, Guatemala. Unpublished report by Wildlife Conservation Society-Guatemala & Centro de Monitoreo y Evaluación del CONAP (CEMEC).

Whitfield, D.P., Fielding, A.H., McLeod, D.R.A., Haworth, P.F., Watson, J., 2006. A conservation framework for the golden eagle in Scotland: Refining condition targets and assessment of constraint influences. Source: Biological Conservation 130: 465-480.

Wiktander, U., Olsson, O., & Nilsson, S.G., 2001. Seasonal variation in home-range size, and habitat requirement of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in southern Sweden. Biological Conservation 100:387-395.

Wisdom, M.J., Mills, L.S. & Doak, D.F., 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

Wood J.R.I., Scotland R., & Hughes C., 2006. Plant endemism of the central Andean valleys, Bolivia. Darwin Initiative Report for 1 October 2002 – 28 February 2006. Department of Plant Sciences, University of Oxford.

Worton, B.J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

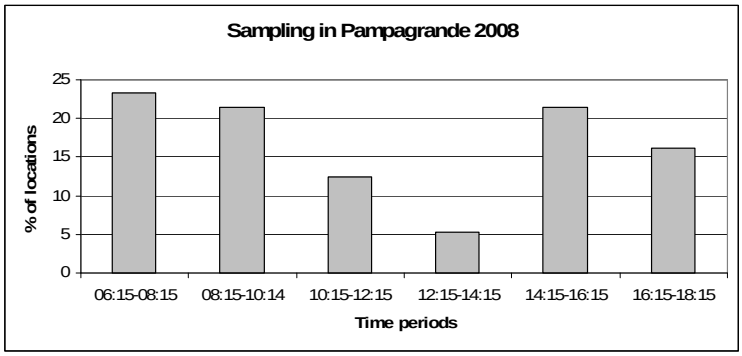
Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Worton, B. J., 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794-800.

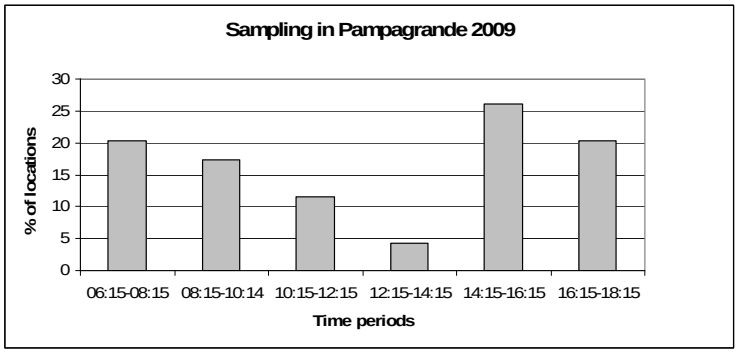
Yamashita, C., 1987. Field observations on the Indigo Macaw (*Anodorhynchus leari*), a highly endangered species from northeastern Brazil. Wilson Bulletin 99:280-282.

Yaremych, S.A., Novak, R.J., & Raim, A.J., 2004. Home range and habitat use by American Crows in relation to transmission of West Nile Virus. Wilson Bulletin 116:232-239.

Appendix



A



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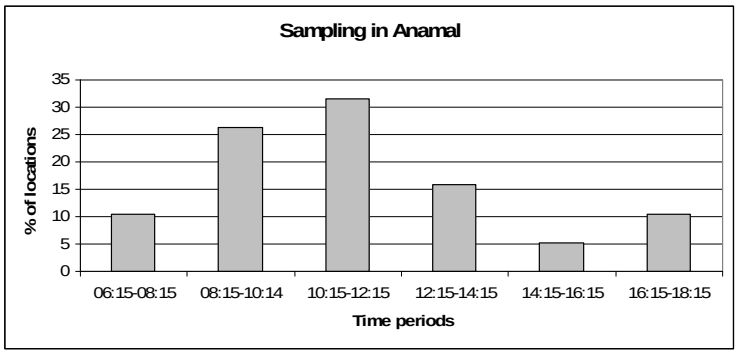

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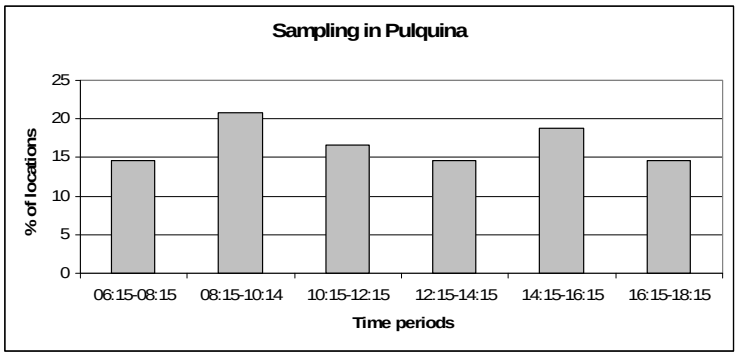
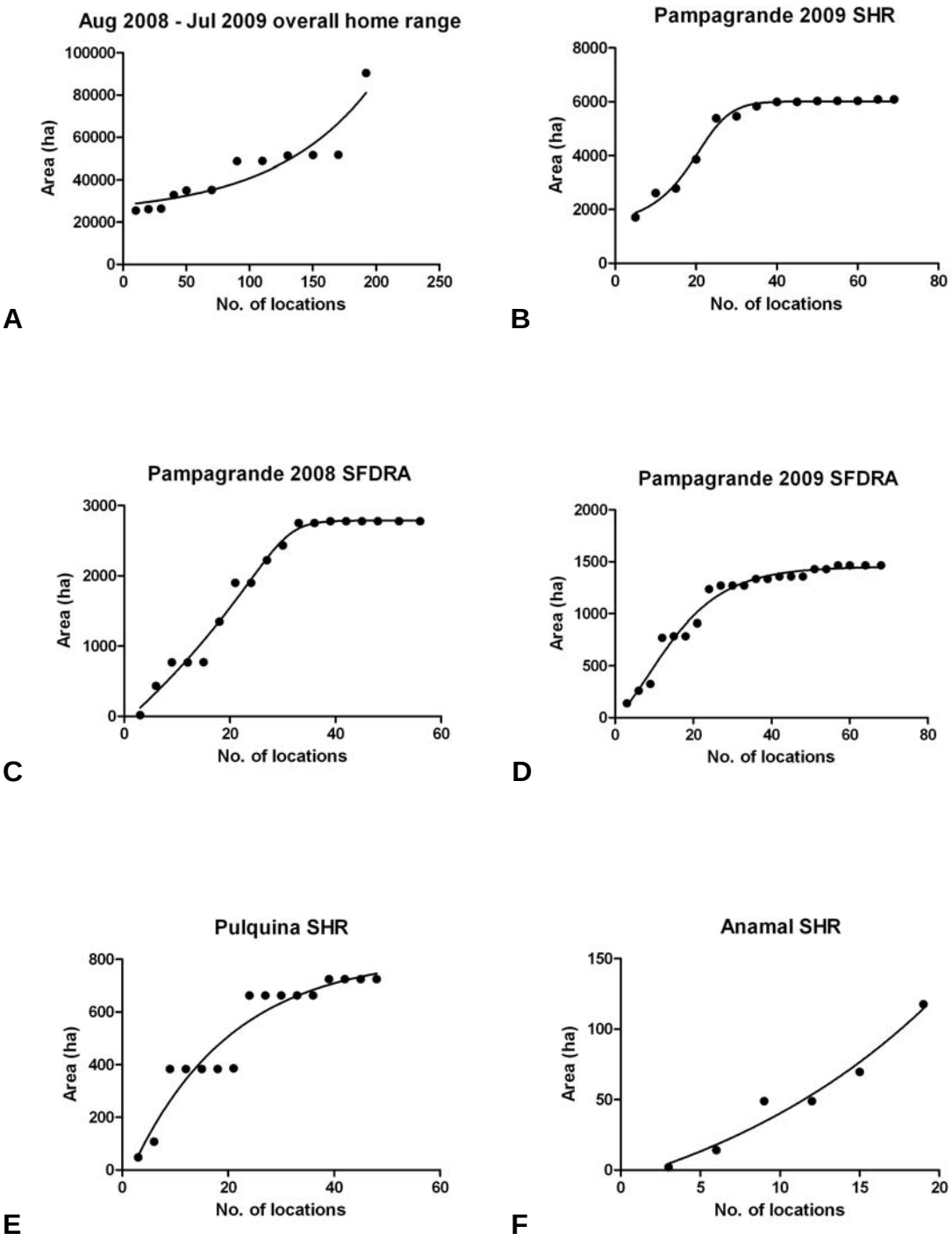
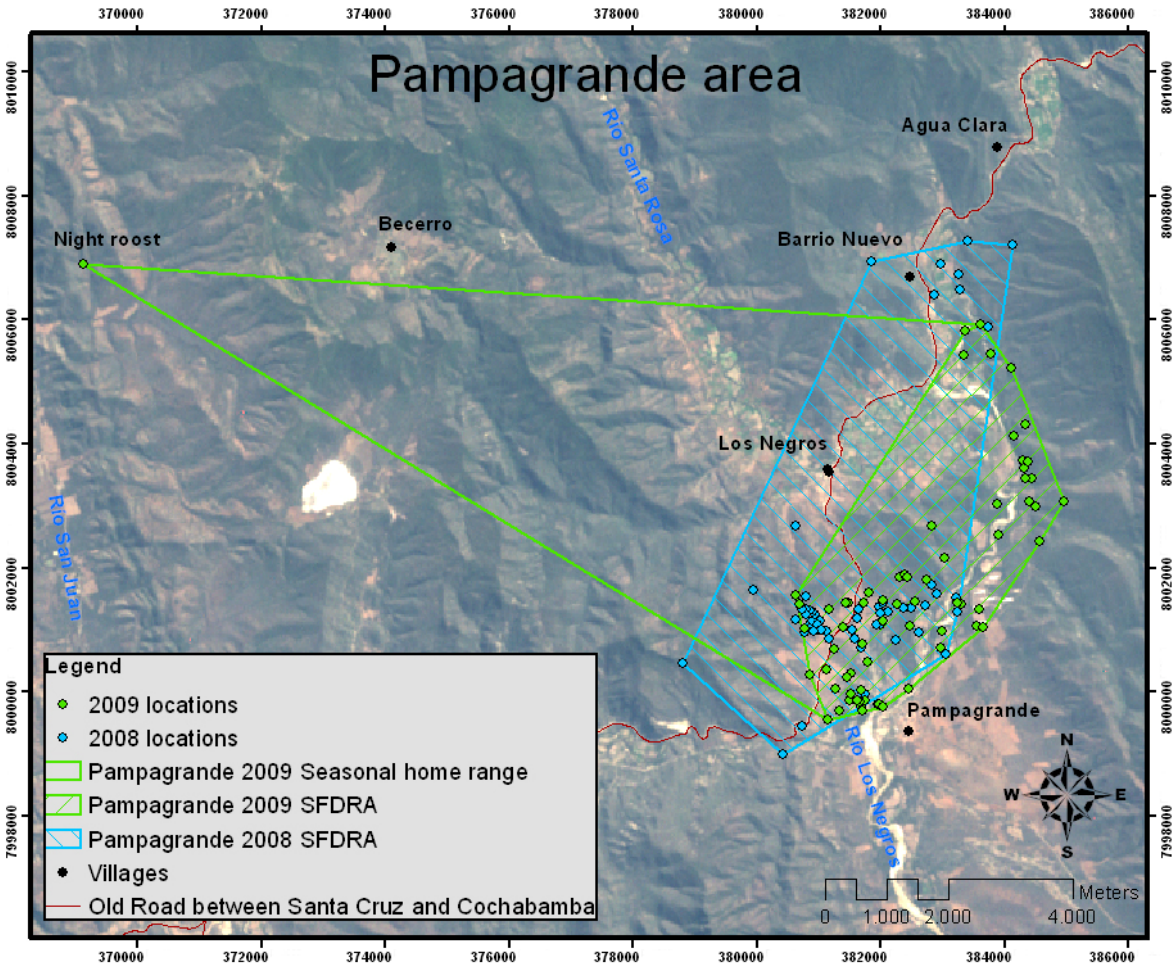


D

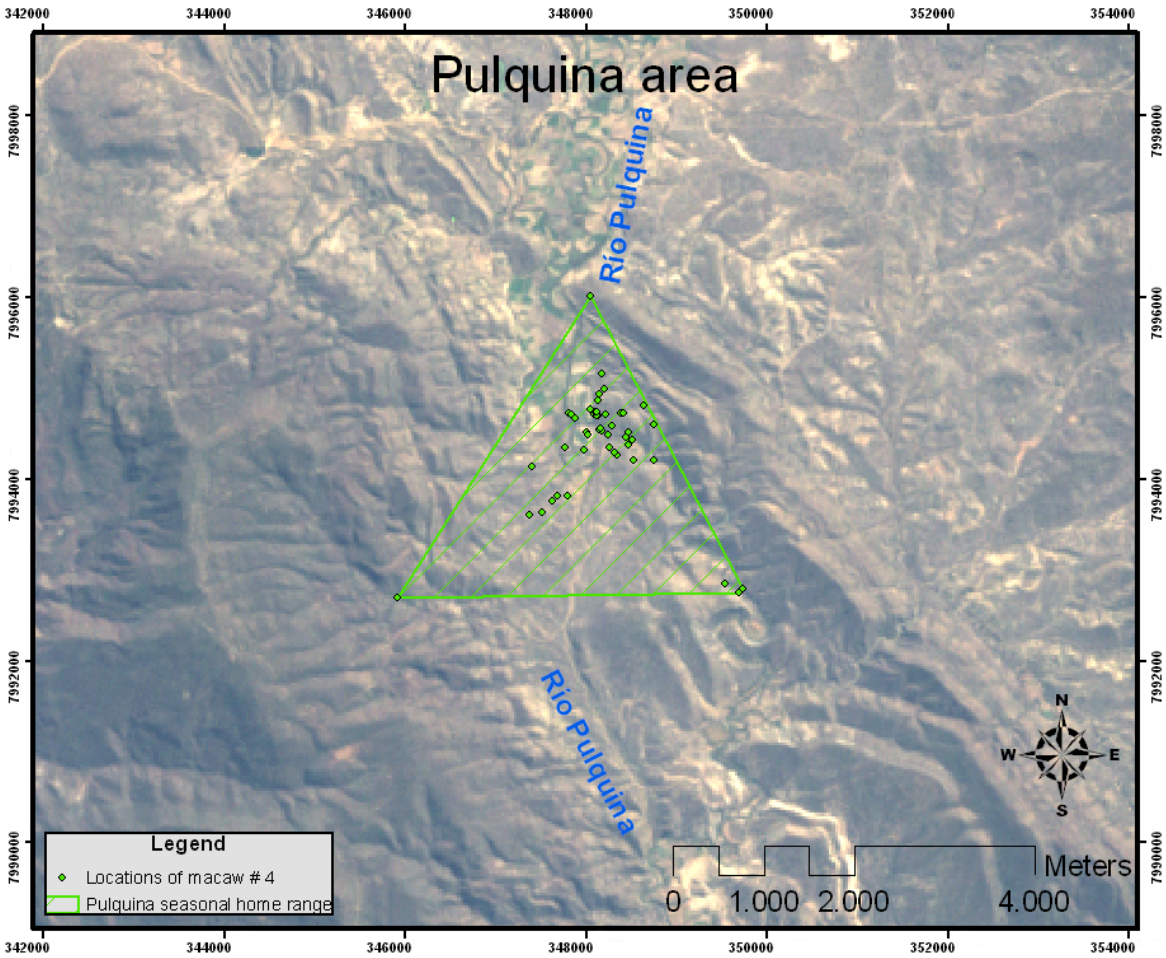
Appendix 1. Histograms of the different ranges showing the frequency distribution of the recorded locations over five two-hour-periods. Asterisks indicate sampling that I consider adequate to represent the macaws' movements during the day. **A** Pampagrande 2008*; **B** Pampagrande 2009*; **C** Anamal; **D** Pulquina*.



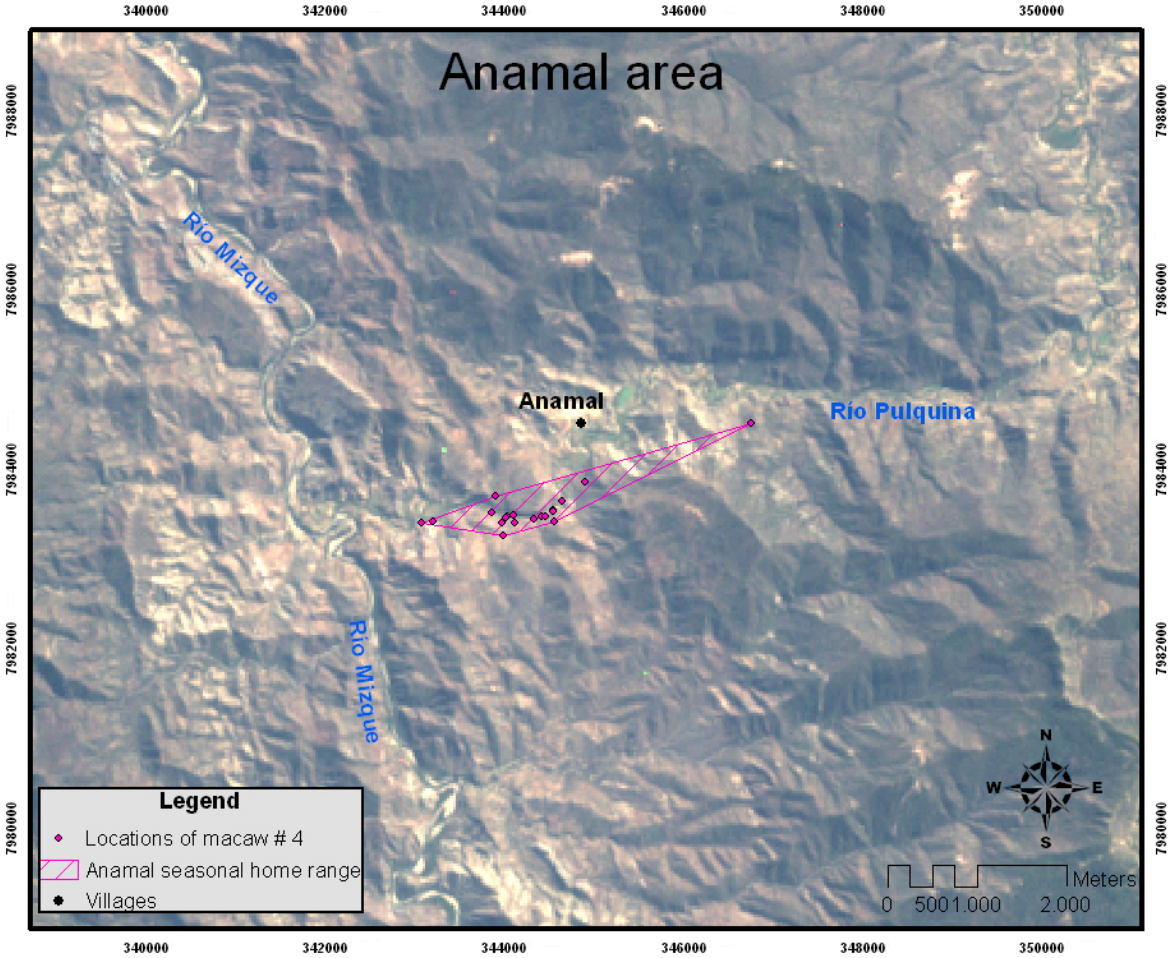
Appendix 2. Observation-area curves of the different ranges. Asterisks denote asymptotic ranges that indicate reliable range estimates. **A** Aug 2008 – Jul 2009 overall home range; **B** Pampagrande 2009 seasonal home range*; **C** Pampagrande 2008 seasonal feeding and daytime roosting area*; **D** Pampagrande 2009 seasonal feeding and daytime roosting area*; **E** Pulquina seasonal home range(*); **F** Anamal seasonal feeding home range.



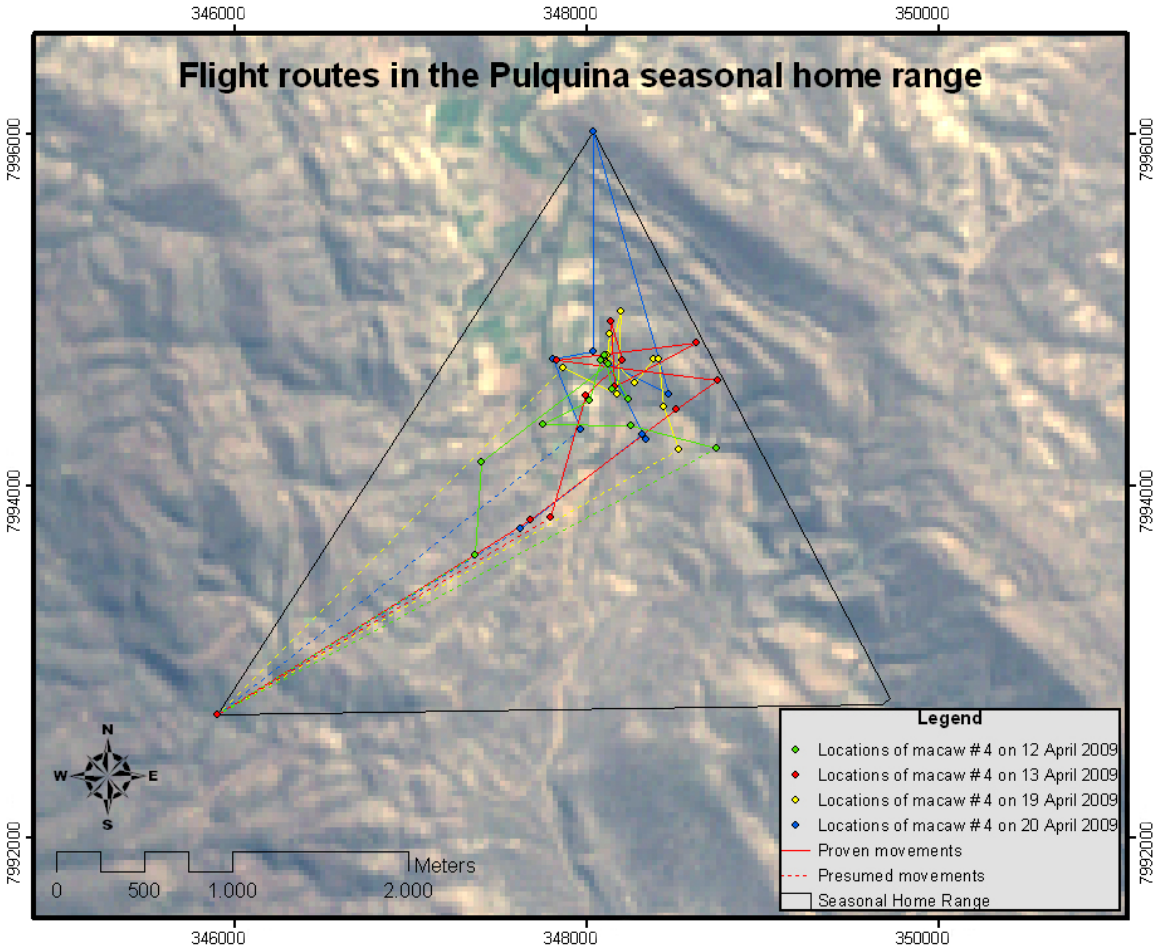
Appendix 3. 2008 and 2009 seasonal feeding and daytime roosting areas and 2009 seasonal home range in the Pampagrande area. The background shows a processed Landsat 7 Enhanced Thematic Mapper Plus satellite Image from August 2001. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).



Appendix 4. Seasonal home range in the Pulquina area. The background shows a processed Landsat 7 Enhanced Thematic Mapper Plus satellite Image from August 2001. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).



Appendix 5. Seasonal home range in the Pulquina area. The background shows a processed Landsat 7 Enhanced Thematic Mapper Plus satellite Image from August 2001. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).



Appendix 6: Daily flight routes of macaw #4 in the Pulquina area. The background shows a processed Landsat 7 Enhanced Thematic Mapper Plus satellite Image from August 2001. Geographic references from Instituto Nacional de Estadística, Bolivia. Geographic Coordinate System: World Geodetic Survey 1984 (GCS WGS 1984).

Appendix 7. A Flock of 214 Red-fronted Macaws flying over a peanut field. Picture taken near Pampagrande.