# PARROT CLAYLICKS: DISTRIBUTION, PATTERNS OF USE AND ECOLOGICAL CORRELATES FROM A PARROT ASSEMBLAGE IN SOUTHEASTERN PERU

A dissertation by

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# ABSTRACT

The parrot family (Psittacidae) is one of the most intelligent, colourful and easily recognisable of the large bird families. They are also one of the most endangered, due to habitat loss; introduction of exotic species and diseases; persecution; hunting and the pet trade. In South America parrots are regularly recorded consuming soil. The reasons for this behaviour have been an issue for debate over the last decade as benefits extend to both the adsorption of dietary toxins and the supplementation of nutrients, most notably sodium.

This study focuses on the species rich parrot assemblage of southeastern Peru, one of the most intact remaining areas of Amazon forest, but one which faces major threats due to mining and the paving of a major road through the area which will most likely be associated with an increase in deforestation rates. Tourism has been recognised as an important potentially sustainable economic activity. Claylicks are a major tourist attraction for the area but boats passing riverside sites visited by parrots are a potential source of disturbance.

In this study, a mapping exercise of the extent of claylick occurrence across South America showed that claylick density and associated species richness were highest in the western lowland Amazon forests and on younger geological formations. Since similar soils occur on the eastern side of the Amazon, this distribution points to sodium being the underlying cause for geophagy as sodium deposition decreases from east to west.

In southeastern Peru, parrot species richness at claylicks also increased westwards. Temporal seasonal patterns for most species were correlated at five claylicks, with the exception of species associated with successional forest types. Daily feeding patterns were strongly correlated among claylicks for individual species. Variation in diurnal feeding may be linked to predator evasion strategies. On a daily basis, 1% of the total population within a 10km radius of a claylick visit the claylick. This level was higher for species associated with successional forests.

A technique is introduced to correct for the Distance sampling assumption that all birds on the line of the transect are detected with certainty (g(0) = 1), whereby correction factors are calculated from vocalisation rates. This technique will improve density estimates for canopy bird surveys in tall forest environments. Density estimates were higher in floodplain forest compared to *tierra-firme* forests, and higher in floodplain forests in the dry season compared to the wet season. A degree of this may be explained by claylick proximity, but there was no difference overall in bird densities at a site in close proximity to a claylick compared to a site further removed from a claylick.

Instead, a phenological study conducted suggests that food availability, especially in the form of flowering trees, may be higher in floodplain forest in the dry season. A wide range of food items was recorded, but seeds, fruit and flower predominated. There was evident niche partitioning among the parrot assemblage at the dietary level. Daily claylick use was not correlated with any dietary metric (dietary breadth, proportion of seeds, rare items in diet, etc.) across the parrot assemblage, but the proportion of parrots in the area using the claylick on a daily basis was correlated for species scoring high on an index of successional forest preference.

Disturbance of feeding activity at claylicks is a concern as the clay is evidently important, especially during the breeding season. It is also in the interest of tourist companies in the area to minimise disturbance in order to maximise viewing opportunities for their tourists. Boats approaching the claylick within 100m were more likely to cause an anti-predatory response compared to boats travelling further away, even though overall a large degree of tolerance or habituation was displayed by the birds. Birds displayed avoidance behaviour when tourists observed a claylick without a blind from less than 100m.

In the study area, many claylicks were faced with no or inadequate protection from poor tourist practise, incidental human perturbation and direct persecution through hunting. This study showed that a large claylick would solicit payments of up to US$100,000 by tourist companies, who could capitalize on their investment by charging entrance fees to other operators or tourists around US$25.00 a visit. As such, establishing ecotourism concessions provide an economic solution to furthering the protection of claylicks.

This study found little indirect evidence for the theory that clay is consumed by parrots to mitigate dietary toxins, although it has previously been established that this is a property of the clay. Large numbers of birds visiting clay on a daily basis is instead better explained by the need to supplement sodium, which is found at low concentrations in plants. Sodium is essential to cell functioning in vertebrates, and is the most likely reason for the spectacular avian displays along the riverbanks of southeastern Peru.

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## 1.1 Introduction

The parrot and macaw family (Psittacidae) is one of the most endangered large bird families in the New World (Bennett and Owens, 1997, Collar, 1997). The Psittaciformes is one of nine bird orders that contains significantly more threatened species than average and the Psittacidae is one of 15 extinction prone families according to IUCN Red List data (Baillie et al., 2004). Forty six (34%) of the parrot species in South America are at risk of global extinction due to habitat loss, fragmentation or degradation; introduction of exotic species and diseases; persecution; hunting and the pet trade (Snyder et al., 2000). They are important flagship species for conservation efforts in Latin America (Snyder et al., 2000, Harris et al., 2005).

Neotropical parrots are distributed from the United States and northern Mexico to Tierra del Fuego at the southernmost tip of South America, and from over 4000m in the high Andes to the lowland forests of Amazonia (Wege and Long, 1995). Neotropical parrots live in many different ecological settings and have evolved different life history traits (Juniper and Parr, 1998). Some species are ecologically flexible and have become established outside their natural ranges, for example the Monk Parakeet *Myiopsitta monachus* (Buhrman-Deever et al., 2007). Other species are restricted to specific habitats; for example the critically endangered Lear's Macaw *Anodorhynchus leari* (Nogueira et al., 2006, Yamashita, 1987). Yet very little is known of their ecology, nesting habits or diets; possibly a consequence of the bias to studies conducted in temperate zones (Bibby et al., 1998). The Neotropical parrot family also appears to engage extensively in avian geophagy as seen in popular articles such as Munn (1994). Yet the first journal publication mentioning geophagy in a Neotropical parrot, according to Web of Knowledge (http://www.isiwebofknowledge.com), is Emmons and Stark (1979), and only eleven publications contain both the word parrot and geophagy.

This thesis aims to further our understanding of the parrot family and their habit of geophagy by concentrating on a parrot-rich community in southeastern Peru, an area also well known for its parrot claylicks. In this chapter I will give a general background to our body of knowledge on the parrot family from a Neotropical perspective; and give a broad introduction to our current state of knowledge on the field of geophagy, with particular reference to avian and parrot geophagy.

## 1.2 Threats to Neotropical parrots

Nineteen parrot species are recorded as extinct by Birdlife (2009), including two *Amazona* species and five *Ara* species. Spix's Macaw *Cyanopsitta spixii* now exists only in captivity (Juniper, 2003). Population declines of parrots today are mostly due to anthropogenic activities. Threats vary geographically, temporally, and with the specific characteristics of the species involved: introduced predators and competitors have been a major threat primarily for parrot populations on oceanic islands; hunting for food is a principal threat for relatively large species; and trade has been extremely damaging for many highly charismatic or colourful species (Snyder et al., 2000).

Tropical parrots, like many tropical species, face continued loss of habitat through destruction of tropical forests (DeFries et al., 2002), the consequences of which can be seen in the rapid avifaunal collapse along the 'Amazonian deforestation frontier' (Lees and Peres, 2006). Of the 95 parrot species considered to be in danger of extinction in a review by Snyder et al. (2000), habitat destruction and fragmentation was believed to threaten 78, while trade endangered 36 species.

The loss of keystone nesting trees through selective logging and the unsustainable harvesting of wild parrots are direct threats due to the loss of current generations (Brightsmith, 2005b). They also have consequences on reproductive success as birds are forced to nest in suboptimal nesting sites more accessible to predators (Koenig, 2001). The recent increased harvest of *Dipteryx panamensis* in Costa Rica is the most probable cause for the decline of Great Green Macaws *Ara ambigua* in that country (Bjork and Powell, 1995, Chassot and Monge, 2002). Commercial timber harvesting appears to have affected nest site availability for Thick-billed Parrot *Rhynchopsitta pachyrhyncha* by leaving few snags and trees large enough for parrots to nest in (Monterrubio-Rico and Enkerlin-Hoeflich, 2004). Most parrots are cavity nesters that require large secondary cavities. A shortage of suitable nesting sites could lead to increased competition resulting in an increase in infanticide and egg destruction (Beissinger et al., 1998). Intraspecific interference competition of nesting macaws may exclude potential breeders from investigating cavities, effectively limiting nest availability where nest sites are clumped in distribution (Renton, 2004).

Continued over-harvesting for the pet trade was, and may still be, a widespread and biologically significant source of nest mortality in Neotropical parrots (Wright et al., 2001). This is the case for many Neotropical species, for example, Yellow-headed Parrot *Amazona oratrix "guatemalensis"* (Eisermann, 2003) and Yellow-headed Parrot *Amazona oratrix "panamensis"* (Rodriguez-Castillo and Eberhard, 2006). Unsustainable harvest of chicks for the pet trade has had severe impacts on populations of Blue-and-yellow Macaw *Ara ararauna,* Scarlet Macaw *Ara macao* and Orange-winged Parrots *Amazona amazonica* in northern Peru (Gonzalez, 2003). The highest daily incomes of communities in that area between 1994 and 1997 came from the extraction of ornamental fishes, turtle eggs and young macaws and parrots (US$ 10-30 per day), so unsustainable harvesting was an attractive source of income compared to agriculture and day labour that resulted in an average daily earning of up to $5 (Kvist et al., 2001).

Peres (2000) estimates that between 65,000 and 159,000 individuals of the *Ara* genus, and 121,000 and 297,000 individuals belonging to *Amazona* genus are hunted and consumed by low-income rural population of Brazilian Amazonia per year. Increased hunting pressure is often associated with road building and logging operations which greatly facilitate access to large, previously inaccessible forest areas and create opportunities for commercial hunting (Fimbel et al., 2001). Mean flock size of macaws and parrots in a Neotropical forest are higher in non-hunted sites than hunted sites, as are encounter rates (Thiollay, 2005). Some species are persecuted directly as crop or invasive pests (Shelgren et al., 1975, Butler, 2003, Warburton and Perrin, 2005, Cockle et al., 2007). The persecution of the Blue-winged Macaw *Primolius maracana* has resulted in its near extermination in Argentina (Bodrati et al., 2006). Whether or not they are preferred targets for hunters or killed opportunistically, macaws and parrots are long-lived with generally low reproductive rates. These are demographic traits that make populations vulnerable when subject to increased mortality (Murphy et al., 2003).

## 1.3 Conservation problems and opportunities

Despite the pessimistic outlook for the parrot family on many fronts, conservation action can help (de L. Brooke et al., 2008). Poaching is significantly lower at protected sites (Wright et al., 2001, Pain et al., 2006). Populations of species that have been classified as threatened can recover, as seen in Indonesia with Citron-crested Cockatoo

*Cacatua sulphurea* after a 10 year ban in international trade (Cahill et al., 2006); and in Costa Rica where populations of Scarlet Macaw *Ara macao* increased and now sustain themselves after collaborative conservation by local stakeholders (Vaughan et al., 2005).

The ecotourism industry has also played its part in parrot conservation by providing alternative forms of employment, as well as education opportunities (Munn, 1992). The authorities of the Windward Islands have recognised that sound environmental management measures can complement rather than hinder national socio-economic goals and objectives resulting in the development of links between parrot conservation and other sectors of the economy (Christian et al., 1996). Suitable conservation strategies incorporating techniques ranging from reintroduction to community participation and education have saved some species, like the Puerto Rican Parrot *Amazona vittata,* from certain extinction (Snyder et al., 1987). With some models projecting the extinction of 6 – 14% of all bird species by 2100 (Sekercioglu et al., 2004), such conservation measures are sorely needed, but require an understanding of the biology, ecology and abundance of the target species.

## 1.4 Breeding and Behaviour

Most parrots nest in cavities in trees (Juniper and Parr, 1998) or cliffs, e.g. Red-fronted Macaw *Ara rubrogenys* (Lanning, 1991). Sixteen Neotropical parrot species also nest in termitaria (termite mounds), but this number may increase as there is a dearth of information on avian nesting ecology (Sanchez-Martinez and Renton, 2009). Competition for nest sites and predation pressure may have favoured a shift from nesting in tree cavities to the exploitation of alternative substrates such as termite mounds for nesting (Brightsmith, 2005a). The reliance of parrots on large hollows for nesting makes them vulnerable to any reduction in this resource (Cameron, 2006).

In southeastern Peru the community of parrots show a wide range of nest use; with Amazonian Parrotlet *Nannopsittaca dachillea* using Bromeliads (O'Neill et al., 1991), *Brotogeris* spp. using termitaria (Brightsmith, 2000), and the majority of the rest for which nesting sites are known (there are still no official recorded nesting sites for Black-capped Parakeet *Pyrrhura rupicola* and Blue-headed Macaw *Primolius couloni*) using natural tree cavities (Brightsmith, 2004b). Further resource partitioning is observed in the larger macaws, with the region’s largest macaw, Red-and-green Macaw

*Ara chloropterus*, monopolising large cavities in *Dipteryx micrantha*; slightly smaller Scarlet Macaw *Ara macao* using cavities in a wider variety of trees; and the Blue-and-yellow Macaw *Ara ararauna* nesting almost exclusively in dead Aguaje palms *Mauritia flexuosa* (Renton and Brightsmith, 2009).

Many parrots species tend to be monogamous (Masello et al., 2002) and are altricial, born with sparse down and therefore totally dependent on their parents for temperature regulation and for food (Juniper and Parr, 1998). The female usually broods the chicks and is often dependent on the male feeding her at the nest (Taylor and Perrin, 2004). There is also little sexual dimorphism between sexes, as is typical for many monogamous birds that form life long pair bonds (Andersson, 1994). Although the predominant colour in parrots is green, some have striking bright, non-carotenoid, feather pigments unique to the family (Stradi et al., 2001) and can indicate the quality and condition of individuals (Masello et al., 2004).

Parrots are social birds, often forming large groups that roost together in monospecific or mixed flocks (Harms and Eberhard, 2003). Parrot flock size depends on species (Whitney, 1996), season (Matuzak and Brightsmith, 2007, Wermundsen, 1999), and time of day (Pizo and Simao, 1997, Wermundsen, 1999, Chapman et al., 1989). For Australian species, Brereton (1971) hypothesised that aridity was positively associated with flocking and this has been postulated as the explanation for large flock sizes of Burrowing Parrots *Cyanoliseus patagonus* in Patagonia (Masello et al., 2006). Westcott and Cockburn (1988) suggested that predation is a more significant predictor of sociality in parrots. Wermundsen (1999) suggests that the Pacific Parakeet *Aratinga stenua* groups are larger in the dry season than in the rainy season to find food more efficiently as well as to better escape predation.

### 1.5 Parrot diet

For the most part parrot species consume seeds and are considered important seed predators (Francisco et al., 2008, Renton, 2006, Galetti, 1992, Gilardi, 1996, Trivedi et al., 2004, Higgins, 1979, Janzen, 1981, Coatesestrada et al., 1993). Seeds are the most nutritious part of most plants being high in protein, minerals, and lipids content (Gilardi, 1996). Several species of parrot have been recorded consuming economically important crops from Brazil nuts *Bertholletia excelsa* (Trivedi et al., 2004) to maize (Romero-Balderas et al., 2006).

Most parrots are frugivorous to some extent (Galetti, 1997), but most species are able to exploit a wide range of food resources, including flowers and nectar (Raguso-Netto, 2006, Cotton, 2001), insect larvae in galls (Martuscelli, 1994, Renton, 2006), termites alates (Sazima, 1989), leaves (Kristosch and Marcondes-Machado, 2001, Greene, 1999), seeds (Roth 1984, Sick 1997, Nemeth and Vaughan 2004, Renton 2006), and carrion (Greene, 1999).

Nectar has been assumed to be a useful energy substitute when fruit is scarce (Terborgh, 1986). Flowers and nectar provide a rich food resource during prolonged dry seasons for parakeets in the Pantanal, Brazil (Ragusa-Netto and Fecchio, 2006). There are a few records of pollination by parrots in the Neotropics (Maues and Venturieri, 1996, Ragusa-Netto, 2002), but generally feeding of flowers has been recorded to be destructive and may even be a reason for mass flowering events as plant species attempt to mitigate damage by flower predators (Ragusa-Netto, 2005).

Many parrots are generalist in their diet and many have proven to be adaptable. In Trinidad the fragmentation of the *Mauritia* palm swamps that provide food for Red-bellied Macaws *Ara manilata* and Orange-winged Parrots *Amazona amazonica* has resulted in them turning to agricultural crops (Bonadie and Bacon, 2000). Several species of parrot have been recorded feeding on introduced plant species, including Yellow-shouldered Parrots *Amazona barbadensis* of Blanquillo, Venezuela (Rodriguez-Ferraro and Sanz, 2007) and Scarlet Macaws *Ara macao* (Vaughan et al., 2006). However, not all species are so adaptable - the serious decline of the Great Green Macaw *Ara ambigua* in western Ecuador has been attributed to, among other pressures, food scarcity (Berg et al., 2007). Dependence on a selective diet makes wild populations vulnerable to changes in food resource availability. Habitat loss may have been the principal factor in the decline of the Carnaby's Cockatoo *Calyptorhynchus funereus latirostris* due to the species' inability to adapt to changes in food resources (Saunders, 1990). Inadequate nutrition has been implicated in poor health and suboptimal reproduction in some parrot species (McDonald, 2003) and parrot populations subject to stress may also be more prone to outbreaks of latent parasites (Deem et al., 2005).

Generally, the parrot family display a wide dietary width. Scarlet Macaws *Ara macao* have been reported to consume 52 food species in the Amazonian rainforest of Peru (Gilardi, 1996). Adult Scarlet Macaws *Ara macao* observed over a five month period in Costa Rica were recorded feeding on 15 plant species from 12 families, with seeds forming 76% of the diet (Renton, 2006). A longer term study of Scarlet Macaws

*Ara macao* in Costa Rica recorded feeding events on seeds, fruits, leaves, flowers and bark of 43 plant species including exotic species introduced as crops (Vaughan et al., 2006, Marineros and Vaughan, 1995).

Low variety in nestling diets is reported for Lilac-crowned Parrots *Amazona finschi* (Renton, 1998), Red-crowned Parrots *Amazona viridigenalis* in Mexico (Enkerlin-Hoeflich and Hogan, 1997) and Scarlet Macaws *Ara macao* (Renton, 2006). The high protein requirement for nestling growth may oblige parent birds to select nutrient-rich resources for the young (Klasing, 1998, Renton, 2006). The role of twigs and bark in all the diets of the species mentioned above, remains to be clarified especially in the light of the fact that few foraging events of these materials has been recorded for adults (Renton, 2006).

Several important studies looking at diet and parrot ecology in Peru have been restricted to specific seasons (e.g. Gilardi 1996) and there is no clear picture on how diet changes through seasons in response to different food source availability even though the availability of food resources may strongly influence parrot local patterns of abundance. Changes in local abundance patterns of parrots can be triggered by seasonal availability of food resources within habitat mosaics (Ragusa-Netto, 2007). Seasonal fruiting events in the Cerrado, Brazil, corresponded to a significant increase of Blue-and-yellow Macaws *Ara ararauna* to the area (Ragusa-Netto, 2006).

## 1.6 Scales of parrot movements

Changes in local frugivorous and granivorous bird populations have been recorded in the tropics in response to changes in rainfall and associated resource availability (Karr, 1976). Parrots forage mostly in the canopy and may periodically experience food shortage due to the seasonal flowering and fruiting patterns in this forest layer, especially in more seasonal forests (Ramirez, 2002), resulting in movements to areas of more favourable food availability (Roth, 1984, Renton, 2001). Seasonal movements of macaws observed in other studies (e.g. Renton, 2002, Karubian et al., 2005) may also be a result of such resource tracking. Parrots are well known for their movements not only in relation to their search for food resources, but also for movements from roosts to foraging areas (Masello et al., 2006, Berg and Angel, 2006, Cougill and Marsden, 2004).

The extent of parrot movements vary from a few kilometres for some species (Ndithia and Perrin, 2006) to hundreds of kilometres in the case of Mealy Parrots *Amazona farinosa* of northern Guatemala (Bjork, 2004). Data from a radio-telemetry study of nesting Great-green Macaws *Ara ambigua* in Costa Rica revealed that some individuals migrate at least 150 km north into southeastern Nicaragua during the non-breeding season (Bjork and Powell, 1995). Radio-collars on Hyacinth Macaws *Anodorhynchus hyacinthinus* show that juveniles disperse up to 35 km after fledging (Seixas et al., 2002). In Australia, the locally nomadic Rainbow Lorikeet *Trichoglossus haemotodus* is able to travel over 100 km in a day (Schodde and Tidemann, 1986). Yellow-lored Parrot *Amazona xantholora* has been recorded making daily crossings of the 20-km wide channel between the Yucatan mainland and Cozumel Island to feed (Griscom, 1926). Distances between Caribbean islands upwards of 90 km appear to be enough to restrict inter-island migration and has resulted in several of these islands having unique species. Altitudinal migration has been suggested for several species including the Blue-bellied Parrot *Triclaria malachitacea* from eastern Brazil (Whitney, 1996), Blue-winged Parrotlet *Forpus crassirostris* of the Atlantic forest of Brazil (Galetti, 1997) and Tucuman Parrot *Amazona tucumana* in subtropical montane forests of Argentina and Bolivia (Politi and Rivera, 2005). Altitudinal migration is a clear example of movement between resources available at different times over a relatively short distance. It is suspected that similar movements may be occurring over larger distances between resources in lowland Amazon forests that have yet to be understood (Renton, 2002).

## 1.7 Estimating parrot abundance

Local movements and migrations make the task of estimating avian abundance difficult. This is especially the case in the tropics where until recently index based counts have been the method of choice (Galetti, 1997) and there are very few comparable abundance estimates across the region. How common are parrots generally and what they contribute to the avian biomass of tropical forests has not been quantified (Snyder et al., 2000). There is also little information on the ecological and life history factors which determine why some species are rare and some common (Walker, 2006).

Where possible for isolated roosting species, roost counts can produce estimates of abundance and recruitment (Rodriguez-Ferraro and Sanz, 2007, Berg and Angel, 2006, Matuzak and Brightsmith, 2007), but these studies assume that the main roosts have been identified and that most of the population uses them. Roost counting has not yet proved to be feasible for providing population estimates for parrot species from tall forested regions of the Amazon. More recently, distance based sampling (Buckland et al., 2001) has become more popular as evidenced by several publications over the last decade (e.g. Marsden et al., 2001, Marsden and Whiffin, 2003, Evans et al., 2005, Marsden et al., 2005). Abundance estimates have now been produced for some parrot species across the globe using these methods (Guix et al., 1999, Walker and Cahill, 2000). However, there are limitations, and for many rare species insufficient encounters are obtained to allow precise abundance estimation (Marsden, 1999) and so only a few studies have produced density estimates for Neotropical parrots (see Guix et al., 1999, Lloyd, 2004, Rivera-Milan et al., 2005).

Population estimates have yet to be produced for most parrot species from southeastern Peru (Table 1.1). Few avian studies have the financial support or time in order to engage in the long-term studies necessary to account for seasonal changes in movement that can result in parts of a species range, for instance around geophagy sites or claylicks (Brightsmith et al., 2008, Brightsmith, 2008).

## 1.8 Geophagy

The consumption of soil or geophagy by a series of taxa from butterflies to elephants has been well documented throughout the world (Jones and Hanson, 1985, Klaus and Schmid, 1998, Wiley and Katz, 1998). Animals deficient in nutrients seek out new foods if it corrects a nutritional deficit or imbalance (Provenza and Villalba, 2006). Soils differ greatly in their chemical properties and physical structure so consumption of soils is highly selective often causing animals to congregate where the best soils are exposed (Diamond et al., 1999, Houston et al., 2001). Up to 35 species of birds and 12 species of mammals gather in large numbers (>1000 total individuals) to eat soil at claylicks in southeastern Peru (Emmons and Stark, 1979, Brightsmith, 2004a). Apart from Psittacidae, other avian families which engage in geophagy include Columbidae (Pigeons) and Cracidae (Guans, Curassows and Chachalacas). Visiting licks is associated with costs for the animal such as energy needed to get to the site (Wiles and Weeks, 1986), increased exposure to diseases due to increased contact among animals and their faeces (Gilardi et al., 1995), as well as increased risk of predation and poaching (Hebert and Cowan, 1971, Klaus and Schmid, 1998). The benefits from visiting licks must outweigh these costs (Kreulen, 1985).

From *in vitro* experiments on captive *Amazona* parrots, Gilardi et al. (1999) showed that soils from regular avian geophagy sites from Peru did not account for many of the reasons that explain geophagy for other taxa. Specifically the soils were not:

(1) useful mechanical aids for grinding food (many bird species swallow pebbles or very coarse soil (>0.5mm) with which to grind ingested food in the gizzard (Best and Gionfriddo, 1991, Gionfriddo and Best, 1995));

(2) ingested by individuals suffering from diarrhoea (diarrhoea can be reduced by the soil mineral smectite (Mahaney et al., 1999));

(3) significant sources of minerals (soil contains a wide array of minerals (Mills and Milewski, 2007), but with the exception of sodium these tend to be higher in the natural diets of the wild parrots of Peru (Gilardi, 1996));

(4) gastric pH buffers (the rumen of domestic livestock can become acidic on a plant diet low in fibre which alkaline soils can neutralize (Jones and Hanson, 1985). pH may be a reason, along with salt and trace element supplementation, African Olive Pigeon *Columba arquatrix* consume soil (Downs, 2006)).

Gilardi et al. (1999) concluded that adsorption of dietary toxins was the primary reason for geophagy for parrots as positively charged alkaloids bound to the negatively charged clay particles preventing them from passing from the digestive track into the bloodstream (Gilardi et al., 1999). Plants are protected by a broad array of chemical feeding deterrents including alkaloids (McKey, 1974). The consumption of soil by parrots may be a step in the evolutionary arms race between plants, which produce toxins to protect their seeds, and animals, such as parrots, which wish to consume them (Diamond et al., 1999).

Sodium (Na) is the most common explanation for geophagy (Weeks Jr and Kirkpatrick, 1976, Tracy and McNaughton, 1995, Holdo et al., 2002, Brightsmith and Munoz-Najar, 2004, Ayotte et al., 2006). Of the elements required for life Na is unique, as most terrestrial plants have little need of Na (Marschner, 1995), while herbivores and decomposers need to amass Na in concentrations 100- to 1,000-fold over the plants they consume (National Research Council, 2005). Sodium is a key component of virtually every mammalian physiological function - as the major electrolyte of the extracellular fluid Na plays a fundamental role in maintaining the volume and composition of every fluid compartment in the body (Danielsa and Fluharty, 2004). In animals, costly Na pumps maintain gradients of cell concentration and membrane voltage, while in plants, potassium, not Na, performs this function (Taiz and Zeiger, 1998). This biogeochemical disconnect between plants and those that eat them suggests that consumers, but not plants, should suffer when Na inputs to ecosystems decline to thresholds where cell function becomes impaired.

In tropical rainforests extensive rainfall promotes leaching (Vitousek and Sanford, 1986), and the Na content of that rainfall decreases exponentially as one travels inland from sources of oceanic aerosols (Stallard and Edmond, 1981, National Atmospheric Deposition Program, 2006). This decline in aerosol deposition has consequences for ecosystem levels of Na: coastal forests in Panama have higher concentrations of Na than the Peruvian Amazon both in freshwater streams and rivers (Kaspari and Yanoviak, 2009) and ants prefer salt baits to sweet baits with increasing distance from coastal influences (Kaspari et al., 2008). Consistent with the hypothesis of Na limitation (Seastedt and Crossley, 1981), leaf litter decomposition rates and the abundance of decomposers and their predators, increase with NaCl fertilization in an inland Amazon forest (Kaspari et al., 2009).

There is no published information on the distribution of claylicks from any part of the world, at any scale, despite being visual spectacles that attract much attention. The phenomenon of hundreds of parrots visiting claylicks in western Amazon has generated interest in bird-watching literature, especially for Peru and Ecuador (e.g. Wheatley 1995, Clements and Shany 2001, Ridgely and Greenfield 2001, Valqui 2004), and mentioned for Dusky-headed Parakeets *Aratinga weddellii* in Colombia (Hilty and Brown, 1986). It is not reported from similar tropical countries to the north such as Venezuela or Suriname (Haverschmidt et al., 1994, Hilty, 2003). There are also no reports of geophagy in parrot species accounts from Argentina (Narosky and Yzurieta, 1989), Paraguay (Hayes, 1995) or Chile (Jaramillo et al., 2003). Nearly all published records of parrot geophagy in South America originate from study sites in Peru (Emmons and Stark, 1979, O'Neill et al., 1991, Munn, 1992, Munn, 1994, Gilardi et al., 1999, Burger and Gochfeld, 2003, Montenegro, 2004, Brightsmith, 2004a, Brightsmith and Aramburu Munoz-Najar, 2004) with the exception of one site in Bolivia (Mee et al., 2005), one site in eastern Ecuador (Duffie, 2003), and one site in central Amazonia Brazil (Roth, 1984).

## 1.9 Parrots and claylicks in southeastern Peru

Peru has an incredible diversity of bird species, with 101 endemics amongst the 1,792 total species (Schulenberg et al., 2007). This includes including 52 parrot species, ten of which appear on the IUCN's Red List of Threatened Species (IUCN, 2007). The parrots occurring in the southeastern department of Madre de Dios are listed in Table 1.1. Focal studies for this dissertation are located in the district of Tambopata, in the department of Madre de Dios, in southeastern Peru. The Tambopata forms part of the Endemic Bird Area 68 'South-east Peruvian lowlands' (Stattersfield et al., 1998). The forest in this region is humid lowland forest, comprising the floristically diverse tall, irregularly inundated floodplain and riverine forest and the less diverse interpluvial *tierra-firme* forest (Puhakka et al., 1992). The Tambopata also falls between the Important Bird Areas of Manu, probably the most species rich protected area on the planet in terms of bird species (925 registered species), and Pampas del Heath (BirdLife International, 2007).

The integrity of the environment in southeastern Peru is under various specific threats. Over 7,000 parrots from 31 different species were traded in a single market in central Bolivia in a one year period with confirmed Peruvian contacts, and this level of trade is also suspected for Peru (Herrera and Hennessey, 2007). Claylicks provide hunters with easy wait and shoot opportunities requiring little effort compared to roaming hunting strategies (Montenegro, 2004). Riverside claylicks are also under threat from small-scale gold mining, where gold miners actively erode river banks, resulting in mercury contamination and widespread siltation of South American streams (Mol and Ouboter, 2003).

Parrots in southeastern Peru face threats from hunting and the timber industry. The two keystone tree species used by nesting parrots in lowland Amazonia in Peru: *Dipteryx micrantha* (Fabaceae) and *Mauritia flexuosa* (Arecaceae) are increasingly logged throughout their range as they are in high demand for hardwood flooring (Toledo and Rincon, 1999, Wood Flooring International, 2003), and the wood is also used to make charcoal (Brightsmith, 2005b). *Mauritia flexuosa* are threatened because local people commonly cut entire trees to harvest weevil larvae *Rhynchophorus palmarum* and fruit (Peters et al., 1989, Vasquez and Gentry, 1989). If food source availability and nesting sites become compromised, then this will have a detrimental impact on parrot populations and the claylick phenomenon. Hunting, mining, timber extraction and large-scale agriculture are all expected to increase due to improved infrastructure through the region resulting from the completion of a highway connecting Brazil to the coastal ports of Peru (Dourojeanni, 2006). This highway may also facilitate growth in more sustainable economic industries such as Brazil nut extraction and ecotourism.

The ecotourism industry is one of the fastest growing in the area (*fide* C. Kirkby, 2009). While the ecotourism industry has suffered declines in the northern rainforest areas of Peru, there has been steady increasing growth in southeastern Peru (*fide* N. Shany, 2007). The added attraction of predictable avian behaviour at geophagy sites may have something to do with this growth as the claylick spectacle is reliable and a proven tourist attraction (Snyder et al., 2000). The industry provides jobs, and in many cases has changed local attitudes towards parrots from being a source of food to now being a resource that will satisfy the expectations of tourists, who in turn are a main source of income for many families (Johnson and Brightsmith, 2003). There is thus an active interest in understanding and conserving parrots and macaws as an integral part of the new local economy. Despite a long history of interest in claylicks in the region (Emmons and Stark, 1979, Munn, 1994) a lack of information on their distribution, ecology and importance to local animal populations has delayed the implementation of management plans and hampered conservation efforts.

Table 1.1: Parrots of the Madre de Dios department in the southeastern Peruvian Amazon. Data on body size was taken from Forshaw (2006); while species names, IUCN conservation status, population estimates and range sizes were obtained from Datazone (BirdLife International, 2009). * represents species as listed by the SACC (SACC, 2010) and Schulenberg (2007). For population estimate (Pop est) of individuals, Uk represents unknown i.e. there is no reliable estimate at this time. For IUCN status LC = least concern, VU = vulnerable, NT = Near threatened.

| Species | Body size (cm) | IUCN status | Pop est x$10^3$ | Range size x$10^6$ km$^2$ |
|---|---|---|---|---|
| Blue-and-yellow Macaw *Ara ararauna* | 86 | LC | Uk | 7.7 |
| Scarlet Macaw *Ara macao* | 85 | LC | 20-50 | 6.7 |
| Red-and-green Macaw *Ara chloropterus* | 90 | LC | Uk | 8.1 |
| Military Macaw *Ara militaris* | 70 | VU | 10 – 20 | 0.28 |
| Chestnut-fronted Macaw *Ara severus* | 46 | LC | Uk | 5.8 |
| Red-bellied Macaw *Orthopsittaca manilata* | 46 | LC | Uk | 7.2 |
| Blue-headed Macaw *Primolius couloni* | 41 | VU | 9.2 – 46 | 0.37 |
| Red-shouldered Macaw *Diopsittaca nobilis* | 30 | LC | Uk | 4.3 |
| White-eyed Parakeet *Aratinga leucophthalma* | 32 | LC | Uk | 8.5 |
| Dusky-headed Parakeet *Aratinga weddellii* | 28 | LC | Uk | 2.3 |
| Peach-fronted Parakeet *Aratinga aurea* | 26 | LC | Uk | 5.7 |
| Black-capped Parakeet *Pyrrhura rupicola* | 25 | LC | Uk | 0.55 |
| Rose-fronted Parakeet *Pyrrhura roseifrons**<br>Painted Parakeet *Pyrrhura picta* | 22 | LC | Uk | 4 |
| Cobalt-winged Parakeet *Brotogeris cyanoptera* | 18 | LC | Uk | 2.6 |
| Tui Parakeet *Brotogeris sanctithomae* | 17 | LC | Uk | 1.7 |
| Amazonian Parrotlet *Nannopsittaca dachilleae* | 12 | NT | 10 | 0.13 |
| Scarlet-shouldered Parrotlet *Touit huetii* | 16 | LC | Uk | 1.8 |
| Dusky-billed Parrotlet *Forpus modestus (sclateri*)* | 12 | LC | Uk | 2.8 |
| White-bellied Parrot *Pionites leucogaster* | 23 | LC | Uk | 3.6 |
| Orange-cheeked Parrot *Pyrilia barrabandi* | 25 | LC | Uk | 3.5 |
| Blue-headed Parrot *Pionus menstruus* | 28 | LC | Uk | 8.5 |
| Orange-winged Amazon *Amazona amazonica* | 31 | LC | Uk | 7.4 |
| Yellow-crowned Amazon *Amazona ochrocephala* | 38 | LC | Uk | 6.6 |
| Mealy Amazon *Amazona farinosa* | 38 | LC | 50-500 | 7.2 |

## 1.10 Overall aim of the PhD

The overall aim of the PhD is to determine the extent of parrot geophagy in South America and at the local scale in southeastern Peru; and examine patterns of claylick use in relation to abundance, diet and human land use to ultimately enable the development of effective and realistic claylick management strategies.

I present my analyses and findings in the following chapters.

**Chapter 2:** Parrot claylick distribution in South America: Do patterns of 'where' help answer the question 'why'?
*Overview:* Locations of parrot claylicks were obtained by a survey from across South America and spatially analysed using the predictive modelling program Maxent. Parrot species use was related to regional and local environmental variables. The implications of the predicted distribution with respect to current theories driving the daily geophagy phenomenon are discussed.

**Chapter 3:** Spatial and temporal patterns of geophagy across a community of parrots in southeastern Peru
*Overview:* Parrot claylick locations from a survey of the rivers of Madre de Dios department in southeastern Peru were analysed to determine their spatial distribution in relation to parrot species richness. Parrot claylick use at the temporal level was monitored at five claylicks. The proportion of birds visiting claylicks was calculated and the results discussed in terms of the need for geophagy across the local population.

**Chapter 4:** Parrot abundance: detectability and variability with claylick proximity, season and habitat type
*Overview:* Parrot abundance was calculated for each species in the parrot assemblage using Distance sampling techniques. A survey of bird vocalizations was undertaken to calculate correction factors for imprecise detection along the sampling line. Parrot abundance is discussed in relation to season, habitat and claylick proximity.

**Chapter 5:** Habitat selection and dietary metrics in relation to claylick use for a parrot community in southeastern Peru

*Overview:* Observations of feeding parrots were conducted both through a formal survey and from incidental encounters, and patterns of fruit availability were observed from marked trees. Claylick use is discussed in relation to habitat specialization and dietary metrics.

**Chapter 6:** Claylicks and people: conservation status and the impacts of tourism

*Overview:* Parrot claylick value was determined from a short survey of tourism operators. Claylick distribution was mapped in relation to protected areas and the role of ecotourism for extending the protected status of claylicks is discussed. The impacts of boat and on foot tourism is determined, with mitigation strategies and claylick viewing best practise proposed.

**Chapter 7:** Lessons learned and future paths.

*Overview:* Key points from previous chapters are discussed with additional reflections. Gaps in our current state of knowledge of parrots and claylick use are discussed.

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# Chapter 2: Parrot claylick distribution in South America: Do patterns of ‘where’ help answer the question ‘why’?

## 2.1 SUMMARY

Geophagy is well known among some Neotropical parrots. The clay apparently adsorbs dietary toxins and/or provides supplemental nutrients. Location data and 23 environmental layers were used to develop a predictive model of claylick distribution using Maxent software. I related species characteristics to claylick use and examined how parrot assemblages using claylicks changed with distance from the centre of claylick distribution. Fifty-two parrot claylicks were reported from an area of ~4 million km$^2$ but over 50% were restricted to a 35,000 km$^2$ region of southeast Peru and northern Bolivia. Claylicks were strongly associated with moist forest on younger (< 65 million year old) geological formations and exposed river banks. The predictive model of claylick distribution matched the reported range well, with precipitation of warmest quarter, land cover, temperature seasonality, and distance from the ocean being most important predictors of claylick presence. Twenty six of a potential 46 parrot species visited claylicks. Species differed greatly in their lick use, but body size, dietary breadth, abundance and other traits were poor predictors of lick use. I am confident that the survey identified the distribution of major parrot claylicks in South America, although less conspicuous parrot geophagy may occur elsewhere. Claylick distribution reflects both underlying geology (allowing claylick formation in only some regions) and the physiological need for geophagy among parrots in different parts of the continent. Data on the latter are inconclusive, but parrot claylick distribution supports the contention that geophagy is related to sodium deficits than to protection from dietary toxins.

## 2.2 INTRODUCTION

The intentional consumption of soil occurs in a range of taxa on all continents, except Antarctica (Brightsmith, 2004). In the Neotropics, large flocks of parrots visit claylicks on a regular basis to ingest soil at clearly defined claylicks (Gilardi and Munn, 1998, Brightsmith, 2004). Most studies of parrot claylicks in South America originate from study sites in Peru (Emmons and Stark, 1979, Gilardi et al., 1999, Burger and Gochfeld, 2003, Brightsmith and Munoz-Najar, 2004) with the exception of single sites in Bolivia (Mee et al., 2005), eastern Ecuador (Duffie, 2003), and southern Amazonian Brazil (Roth, 1984). Parrot geophagy sites have also been recorded in Mexico (Valdés-Peña et al., 2008), Congo (May, 2001) and Papua New Guinea (Diamond et al., 1999; Symes et al., 2006).

The function/s of geophagy among birds have been discussed in more detail in chapter 1 (Wink et al., 1993; Diamond et al., 1999; Sanders and Jarvis, 2000; Symes et al., 2006). In summary, many bird species consume grit for mechanical digestion of seeds and insects (Verbreek, 1994, Gionfriddo and Best, 1995, Lopez-Calleja et al., 2000), whereas two hypotheses have been proposed to explain the consumption of fine clay soils: 1) clay protects the birds from toxins and/or digestion inhibiting plant secondary compounds in their diets (Diamond et al., 1999; Gilardi et al., 1999) and 2) clay is a source of essential minerals such as sodium (March and Sadleir, 1975; Brightsmith and Munoz-Najar, 2004). Both functions may be important but it is unclear if one of these physiological drives results in the daily phenomenon of many parrots visiting claylicks. No study to date has examined claylick use and distribution at a regional or continent-wide scale.

### 2.2.1 Aim

To determine the spatial distribution of claylicks and their species richness across South America and explain why claylicks are distributed as they are in respect to environmental factors, site availability and the physiological need for geophagy. To achieve this aim I have the following objectives:

1. Identify known claylick locations across South America and model the probable extent across the continent
2. Identify claylick characteristics that influence parrot species richness
3. Identify differences in the parrot assemblages using claylicks
4. Identify characteristics of individual species that use claylicks

## 2.3 METHODS

### 2.3.1 Survey of claylick locations

Information on South American claylick distribution was collected from March to August 2007 through a formal survey of ornithological experts via personal contact and posting on popular forums (see chapter Acknowledgements for respondents' names). Published scientists and bird tour operators from all major South American countries were contacted (except French Guiana). Respondents were asked for the following information: 1) local name of the claylick; 2) geographical location; 3) the position of the claylick (major riverbank, stream or within forest); 4) height and width of the exposed soil surface; 5) number of visits made by respondent to the claylick; 6) the largest number of parrots recorded on the claylick; 7) species observed on the claylick. Sites that were used by only one parrot individual were excluded as they fall outside the scope of regular avian geophagy.

Generic search engines (e.g. Google) were used to search for instances of the words: colpa, collpa, lick, saladero, barreiro, parrot and macaw. Trip reports for South American countries from the birding portal www.travellingbirder.com were also searched.

Where GPS coordinates were not provided information from nearest towns, rivers and associated travel times were used to calculate approximate locations. Information provided was either useful as location data that was used for distribution modelling, while a smaller subset of responses included species claylick use data and information on local site conditions and associated species assemblages.

### 2.3.2 Environmental variables and claylick distribution

Claylick locations were mapped using ArcGIS version 9.2 (ESRI, Redlands, California, USA). 100% minimum convex polygons (MCPs), as well as 75%, 50% and 25% MCPs, were mapped for claylicks based on a system of elimination of the furthest outlying locations. A 'centre of distribution' for claylicks was calculated by selectively rejecting outlying claylicks using MCP tools until a cluster of six claylicks within 25 km of each other was reached. A GIS database (Hearn et al., 2000) was used to overlay geographical information on the claylick locations to determine their distribution in terms of the following: 14 major habitats (relatively large areas of land or water that share a large majority of their species, dynamics, and environmental conditions), 25 land cover types (derived from the U.S. Geological Survey's ‘Global Land Cover Characteristics’ database), 29 geological ages and 90 geological provinces. The geological provinces can be broadly grouped into basins, which represent 24% of South America, and shields and other provinces which represent 26% (Hearn et al., 2000). Chi-squared tests were used to compare the observed and expected claylick distribution between geological age groups and between shields and basins.

### 2.3.3 Predicting claylick distribution

I used the machine learning method Maxent (Phillips, 2005) to predict the spatial distribution of claylicks across South America. Maxent has been used in many areas of species distribution modelling based on locations; for example, locality information from herbarium specimens (Dudık et al., 2004, Phillips et al., 2006, Phillips and Dudik, 2008), and I extend this use to claylick locations. Maxent can handle continuous and categorical variables, and non-linearity and interactions among predictors, making it well-suited for species distribution modelling (Phillips et al., 2006), especially with small sample sizes (Hernandez et al., 2006). Maxent identifies cells with suitable conditions for occurrence (Phillips, 2006), with the importance of individual environmental variables (training gains) based on decreases in gains when that predictor is omitted from the predictor set.

Predictor variables included 19 bioclimatic variables from WorldClim database (Hijmans et al., 2005). These Bioclim variables (~1 km spatial resolution), were generated from monthly averages of minimum, maximum, and mean temperatures, and average precipitation for the period 1950-2000 (Hijmans et al., 2005, Nix, 1986). Vegetation continuous field (VCF) products generated using optical remote sensing data from the Moderate Resolution Imaging Spectroradiometer (MODIS) (Hansen et al., 2000) were used, as were Advanced Very High Resolution Radiometer (AVHRR) land use and land cover map as categorical predictors (Hansen et al., 2003). In addition, the U.S. Geological Survey’s Hydro-1K variables elevation, slope, aspect, flow accumulation, flow direction and compound topographic index were included. Aspect was converted into two linear and orthogonal gradients- northness (cos (aspect)) and eastness (sin(aspect)) (Kumar et al., 2006). Euclidean distance from the Pacific and the Atlantic oceans were calculated as a surrogate for the influence of nutrient deposition from precipitation events using a South American continent boundary shapefile in ArcMap using ‘Euclidean distance’ function in Spatial Analyst. Variables that had different spatial resolution (e.g. MODIS data; 500m resolution) from Bioclim variables were resampled to ~1 km resolution (using bilinear method) to match the resolution for Maxent analysis.

The 40 data layers were distilled to a set of less correlated variables, after assessing cross-correlations (Pearson product-moment correlation coefficient, r) among predictors (Neter et al., 1996) based on 1,050 localities - 50 claylick locations and 1,000 randomly generated points from the northern half of South America (Buermann et al., 2008). Only one variable from a set of highly correlated ($r \geq 0.9$) variables was used in the analyses. The decision to drop or include a variable was made by considering the ease of interpretation and the biological relevance with the claylick distribution. The resulting variable set contained 23 environmental layers (Appendix 2.1).

### 2.3.4 Correlates of claylick use by parrots

Parrot species range maps from Juniper and Parr (1998) were overlaid onto the location of each claylick to provide a comparable measure of a claylick’s potential species richness. Although not entirely accurate for all species, these are consistent and considered superior to other similar sources in a recent macroecological mapping exercise (Blackburn et al., 2004, Mathias et al., 2004).

For each parrot species whose distributions overlapped at least one claylick, range size data was obtained from Birdlife International species accounts (BirdLife International, 2007). As this was not available for the Amazonian Parrotlet *Nannopsittaca dachilleae,* range size was calculated by remapping the species map in Juniper and Parr (1998) with ArcGIS. A measure of relative abundance was calculated for each species as follows: rare = 1, uncommon = 2, common = 3, and abundant = 4 (Birdlife International, 2007). An index of habitat breadth (excluding urban) was created by summing the species’ presence according to Juniper and Parr (1998) in the following six categories: 1) Andean foothills or cloud forest; 2) lowland or humid forest including Atlantic rainforest, varzea and *tierra-firme*; 3) gallery forest; 4) savanna; 5) cultivated; 6) woodland including cerrado, caatinga, chaco or deciduous forest. An index of dietary breadth was calculated by summing, for each species, the incidences of known feeding on the following ten dietary categories as listed in Juniper and Parr (1998): palm (fruit pulp and or seeds); other nuts; leaf or flower buds; berries; fruit; seeds; flowers including blossoms or nectaries; grain crops; insects; other (e.g. bark, leaves). These data were supplemented with field observations from Peru for Black capped Parakeet *Pyrrhura rupicola* and Blue-headed Macaw *Primolius couloni* (Chapter 4), for which Juniper and Parr (1998) listed no information. Mean weight for species was obtained from Dunning (2008).

Mann-Whitney U tests were used to compare species attributes (body weight, range size, ranked abundance, habitat and dietary breadth) for claylick users and non claylick users. Spearman's rank correlations were used to look for relationships between the proportion of licks used by lick users and body weight, abundance, range size, number of licks within range, and dietary and habitat breadth.

### 2.3.5 Parrot community analysis

A non-metric multidimensional scaling analysis (NMDS: CAP, Pisces Conservation Limited, 2002) was used to compare parrot community composition across claylicks. NMDS maximizes rank-order correlation between distance measures and distance in ordination space. NMDS has several advantages over other ordination methods, since it does not assume linearity of the data and it does not require data transformation (Clarke, 1993). Analysis was run using the Sørensen index as the distance measure, a PCA (Principal Component Analysis) starting configuration, a maximum of six axes, with 200 iterations, and a final solution (number of axes) determined by minimising stress (McCune and Grace, 2002). A Spearman's rank correlation analysis was performed between the scores on axes 1 and 2 and distance from the centre of distribution of the claylick.

## 2.4 RESULTS

### 2.4.1 Claylick locations

Locations of 62 claylicks were received. One response, providing the locations of 33 claylicks from the Los Amigos river system in southeast Peru, was excluded to avoid any adverse effects upon modelling results through sample selection bias (Phillips, 2008). Birdwatching trip reports yielded no additional claylicks, but internet searches led to the location of two additional claylicks. Ten locations were discarded due to potential location repetition or poor data quality, leaving 52 claylick locations (Figure 2.1). Two locations were removed during GIS analyses to maintain only one presence location within a 1x1 km pixel (i.e. the spatial resolution of predictor variables).

### 2.4.2 Reported distribution of claylicks

Claylicks occurred in Paraguay, Peru, Bolivia, Brazil and Ecuador, and were concentrated in Amazon rainforest along the eastern base of the Andes in Ecuador and Peru. No parrot geophagy sites were reported from the following areas, and their absence was checked with the following individuals: Argentina (*fide* E.H. Bucher, J.F. Masello); Atlantic Rainforest (*fide* M. A. Pizo, S. Marsden); central Amazonian Brazil (*fide* A. Whittacker); the Pantanal region (*fide* I. Pfeifer); Suriname (*fide* J.H. Ribot); and Venezuela (*fide* D. Ascanio, S. Beissinger).

All reported claylicks were within the ‘tropical and subtropical moist broadleaf forest’ (TSMBF) habitat type, with all but one claylick occurring in the ‘evergreen broadleaf forest’ land cover type (a single claylick in Bolivia was in ‘deciduous broadleaf forest’).

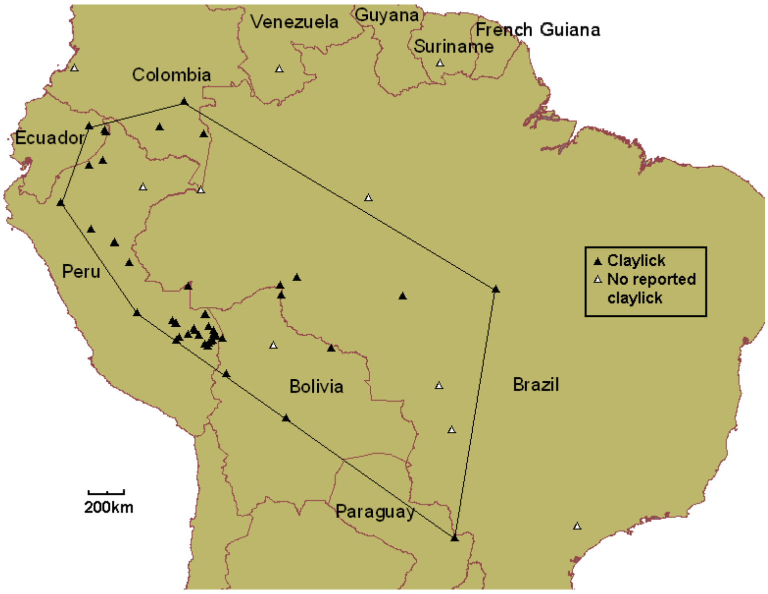

Figure 2.1: Distribution of known parrot claylicks in South America (with 100% Minimum Convex Polygon) in relation to areas with no parrot claylicks. For 25 claylicks at known altitudes, all are below 1000m and all but three are below 500m.

The 100% Minimum Convex Polygon (MCP), which contained all claylicks, was 3.87 million (M) km$^2$. The 75% MCP was only 0.60M km$^2$ (15.6% the area of the 100% MCP), and the 50% MCP was just 0.035M km$^2$ (< 1% of the 100% MCP). Most claylicks were found in southeast Peru (Figure 2.1). The 100% MCP covered 18 geological provinces, of which nine contain claylicks. More claylicks than expected (43) occur within geological basins than on shields ($\chi^2_1 = 29.4$, $P < 0.001$), when considered as a proportion of the total area of TSMBF. The 100% MCP included 17 different geological ages as classified by Hearn et al. (2000), but claylicks were found in only seven. More claylicks than expected ($\chi^2_2 = 12.5$, $p = 0.002$) occurred in younger geological age groups (< 65 million years old), which contain 43 (83%) of the claylicks yet covered only 60% of the total area (Table 2.1).

Table 2.1: Age of geologic settings for South American claylicks. The proportional area of South America is from Hearn et al. (2000). Significantly more claylicks than expected occur in Quaternary and Tertiary regions than in older age groups ($\chi^2_2 = 12.5$, $p = 0.002$).

| Age grouping | Age range (millions of years) | Proportional area of South America | Reported claylicks | Expected claylicks |
|---|---|---|---|---|
| Quaternary | 1.8-0 | 0.31 | 20 | 16 |
| Tertiary | 65-1.8 | 0.29 | 23 | 15 |
| Precambrian to Tertiary | 4500-65 | 0.40 | 8 | 20 |

### 2.4.3 Predicted distribution of parrot claylicks

The Maxent predicted distribution of claylicks (Figure 2.2) showed broad agreement with their known distributions, suggesting that the sampling was adequate for predicting the current distribution. Bio18 (precipitation of warmest quarter; 31.3 %), Land cover (20.4 %), Bio 4 (temperature seasonality; 12.1 %), distance from ocean (7.2%), and MODIS herbaceous cover (4.8%) contributed most to the Maxent prediction. Area under the receiver operating characteristic curve (AUC) was used to evaluate performance of the model at all possible thresholds, and to compare among algorithms (Phillips et al., 2006). Ten random subsets of the data were created with 80% of the data (40 records) used for training the model and 20% of the data (10 records) used for testing the model performance. The mean test AUC was 0.94 (AUC range 0.85 – 0.99), which shows that the model predictions would be correct 94% of the time in finding claylicks at locations where they are predicted to be present. The final model was run using all the data (50 records) (Figure 2.2).

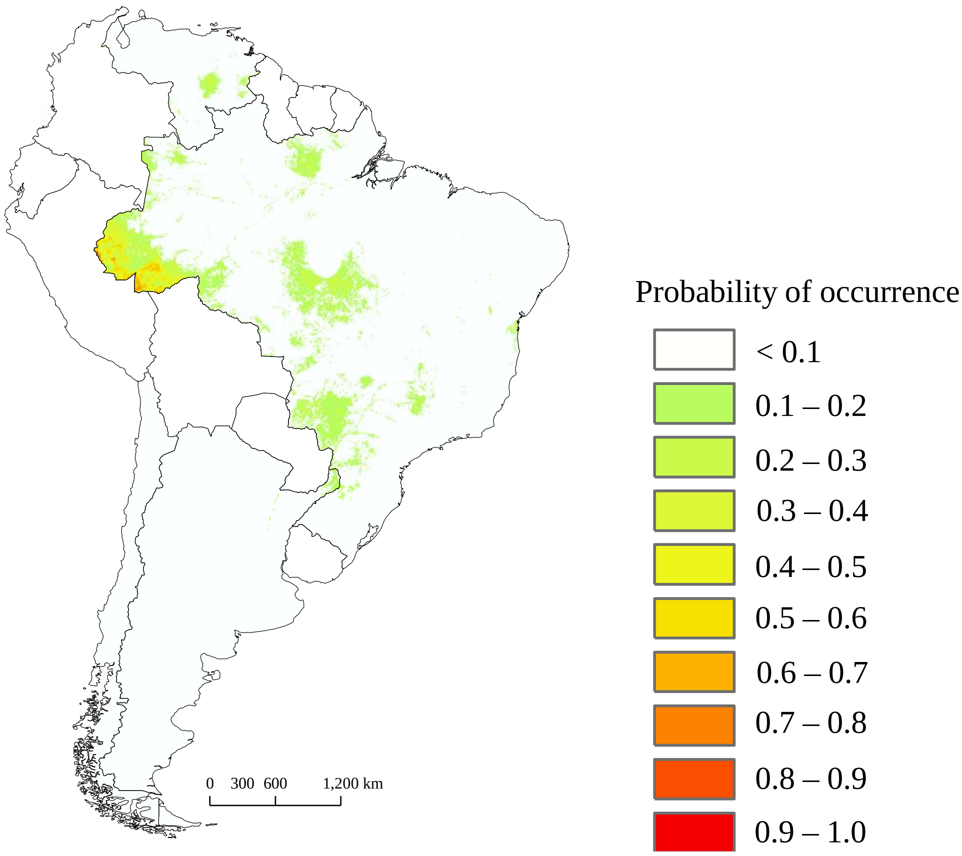

Figure 2.2: Predicted probability of occurrence of parrot claylicks in South America as determined by the Maxent model using 23 environmental variables. Red regions are areas with highest probability of claylick occurrence.

### 2.4.4 Physical characteristics of claylicks used by parrots

Physical attributes of claylicks were reported for 27 sites (Table 2.2), of which 20 were located on the banks of large rivers, five on stream banks and two in forest interiors. Mean claylick height was 10.8 ± 9 m (n = 26) and width was 91 ± 139 m (n = 26), indicating much variation in dimension across sites. There was a significant positive correlation between number of monitoring visits and number of parrot species recorded at claylicks ($r_s = 0.51$, $p = 0.01$, n = 25), so only the 18 claylicks that had been visited nine or more times were included in the subsequent analyses (the correlation between species richness and visitation was no longer significant at this level; $r_s = 0.33$, $p = 0.19$, n = 18). There were significant positive correlations between claylick area and species richness ($r_s = 0.501$, $p = 0.034$, n = 18) and maximum number of individuals recorded

($r_s = 0.74$, $p = 0.001$, n = 17). Maximum number of parrots was correlated with distance to centre of claylick distribution ($r_s = 0.53$, $p = 0.029$, n = 17).

Table 2.2: Claylick physical and bird use characteristics for sites where detailed information was available. No map references are given in order to protect sensitive sites.

| Name | Country | Type | Lick height (m) | Lick width (m) | Max # birds seen | Total number of species on lick | Potential # of parrot species in area | Distance to centre of distribution |
|---|---|---|---|---|---|---|---|---|
| Vallee de la Luna[1] | Bolivia | River | 35 | 150 | 1,044 | 6 | 15 | 700 |
| Flor de Oro[2] | Bolivia | Forest | 0.5 | 25 | 5 | 1 | 25 | 250 |
| Tuichi[3] | Boliva | River | 10 | 20 |  | 1 | 22 | 200 |
| Cristalino Saliero[4] | Brazil | Stream | 0.2 | 25 | 10 | 1 | 21 | 1,800 |
| Rio Madeira[5] | Brazil | River | 10 | 15 | 200 | 3 | 19 | 500 |
| Aripuana[6] | Brazil | River |  |  | 1,000 | 5 | 20 | 1,200 |
| Yasuni[7] | Ecuador | River | 15 | 30 | 80 | 2 | 20 | 1,550 |
| Saladero de las loras[8] | Ecuador | River | 7 | 2 | 20 | 3 | 21 | 1,450 |
| Tiputini colpa de loras[9] | Ecuador | River | 8 | 6 | 30 | 2 | 21 | 1,450 |
| Tiputini colpita pericos[9] | Ecuador | River | 10 | 15 | 100 | 6 | 21 | 1,450 |
| Mbaracuya[10] | Paraguay | Forest | 1 | 12 |  | 1 | 13 | 1,900 |
| Heath[11] | Peru/Bolivia | River | 6.25 | 44.5 | 350 | 12 | 24 | 50 |
| Pantiacolla[12] | Peru | River | 20 | 200 | 500 | 9 | 21 | 200 |
| Blanquillo[13] | Peru | River | 20 | 40 | 100 | 8 | 21 | 150 |
| Mascoitania[14] | Peru | River | 25 | 55 | 100 | 11 | 21 | 250 |
| Rio Blanco[15] | Peru | River | 4 | 12 | 150 | 10 | 21 | 150 |
| Explorer's Inn[16] | Peru | River | 4 | 10 | 180 | 11 | 21 | 50 |
| Colpa Hermosa[17] | Peru | River | 10 | 30 | 350 | 12 | 21 | 50 |
| Manu[18] | Peru | River | 12 | 350 | 600 | 10 | 21 | 150 |
| Colpa Chuncho[17] | Peru | River | 10 | 400 | 800 | 13 | 21 | 50 |
| La Cachuela[17] | Peru | River | 10 | 300 | 250 | 5 | 21 | 0 |
| El Gato[19] | Peru | Stream | 12 | 50 | 150 | 12 | 21 | 50 |
| Colpita Posada[20] | Peru | Stream | 5 | 20 | 150 | 10 | 21 | 50 |
| Piedras LPBS[21] | Peru | River | 18 | 28 | 400 | 12 | 21 | 50 |
| Refugio[22] | Peru | Stream | 1 | 25 | 20 | 2 | 21 | 50 |
| Colpa Colorado[23] | Peru | River | 27 | 500 | 1,400 | 16 | 21 | 100 |
| Tarapoto[24] | Peru | Stream | 1 | 2 | 25 | 2 | 20 | 1,000 |

Respondent or paper: [1]Mee et al. (2005), [2]R. Wallace, B. Hennessey, [3]B. Hennessey, [4]A. Lees, [5]M. Cohn-Haft, [6]Roth (1984), [7]D. Luther, [8]G. Banda-Cruz, [9]J. Fabara, [10]M. A. Morales, [11]P. Nunez, C. Kirkby, P. Donahue, O. Doest, M. Berrocal, [12]W. ten Haven, [13]B. Quispe Estrada, H. Lloyd, [14]C. Torres, [15]O. Doest, [16]V. Vysna, [17]A. Lee, [18]Burger and Gochfeld (2003), [19]Hammer, [20]Y. Quispe, [21]E. Hume, [22]C. Cosmopolis, [23]K. Quinteros, [24]R. Ahlman

### 2.4.5 Correlates of claylick use among parrots

Twenty six of a potential 46 species (57%) (13 of 17 genera) whose range overlapped with at least one claylick were reported as using one or more claylicks (Appendix 2.2). Of the genera with more than three species (*Amazona, Ara, Aratinga, Brotogeris* and *Pyrrhura*), half or more of all species visited claylicks, except for *Amazona* (3 from 8). All five *Ara* species visited claylicks.

Species using claylicks had larger ranges than non-users (claylick users: 4.25M ± 2.99M km$^2$, non-users: 2.12M ± 1.58M km$^2$; $U = 142$, Z = 2.19, $p = 0.029$). There was no difference between users and non-users in terms of body size (claylick users: 322 ± 378 g, non-users: 192 ± 118 g; U = 244, Z = 0.069, $p = 0.95$), habitat breadth (claylick users: 2.8 ± 1.3, non-users: 2.9 ± 1.4; $U = 257$, Z = 0.07, $p = 0.95$), dietary breadth (claylick users: 3 ± 1.1, non-users: 2.7 ± 1.1; U = 187, Z = 0.99, $p = 0.33$), or ranked abundance (claylick users: 2.9 ± 0.7, non-users: 2.9 ± 0.7; U = 245, Z = -0.06, $p = 0.95$). Within those 26 species using claylicks, the mean proportion of available claylicks (those within the range of the species) used was 0.44 ± 0.24, with proportion of claylicks used significantly correlated with habitat breadth ($r_s = 0.40$, $p = 0.045$), but not with range size ($r_s = 0.18$, $p = 0.37$), ranked abundance ($r_s = 0.06$, $p = 0.77$), or dietary breadth ($r_s = 0.29$, $p = 0.17$).

### 2.4.6 Differences in parrot community composition across claylicks

Claylicks and their species composition range from unique single species claylicks to multi-species claylicks with member species represented at most claylicks. The assemblages of claylick-using parrots (axes 1 and 2 of the NMDS) were significantly correlated with distance from the claylick centre of distribution (axis 1: $r_s = 0.42$, $p =$

0.037, n = 25; axis 2: $r_s = 0.42$, $p = 0.037$). Licks near the centre had higher diversity while most outlying claylicks were used by relatively few species (Figure 2.3).

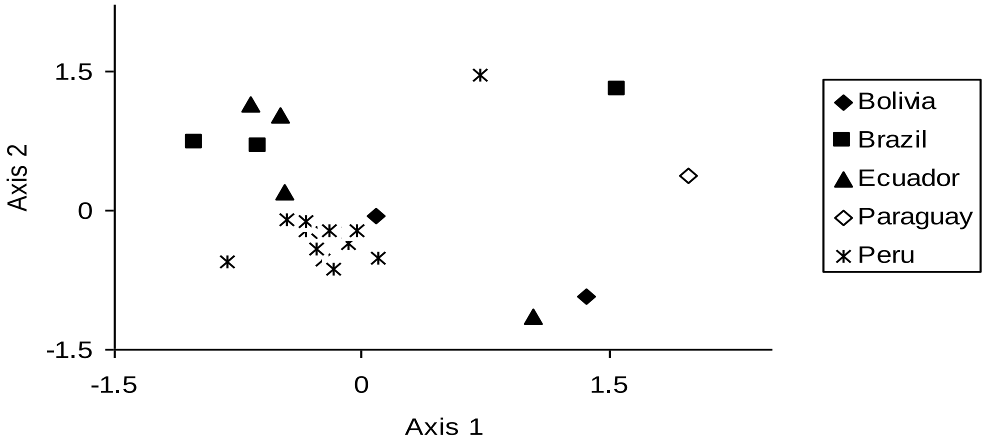

Figure 2.3: Non-metric multidimensional scaling (NMDS) visual interpretation of scaled distances (Axis 1 v Axis 2) for 25 claylicks based on similarity of species composition (STRESS = 0.17). Claylicks are defined by country as an indication of spatial proximity. The only major cluster indicating a community relationship is based around the claylicks of Peru, Ecuador and western Brazil. Outliers are typified by claylicks with low species richness.

## 2.5 DISCUSSION

### 2.5.1 Did the survey capture claylick distribution across South America?

Most parrot claylicks were reported from the forest ecozones of the western Amazon basin in Bolivia, Peru, Ecuador, Brazil and Colombia. The claylick locations received may be biased due to a range of issues including site accessibility, survey outreach, and associated demographics of respondents. However, extensive efforts were made to follow up on regions where no claylicks were reported. Few responses were received from Colombia and large claylicks may exist unreported in this country. Isolated geophagy incidents occur outside the range reported here, for instance Green-rumped Parrotlet *Forpus passerinus* eat soil in Venezuela, but this is rare and unusual (*fide* S. Beissinger). Overall, I am confident that regular parrot geophagy is a western Amazon phenomenon.

The analysis captured the distribution well enough because predicted distribution with >70% probability and real location data did not differ greatly. The Maxent model predicted little extension of the reported range, apart from extrapolations into ‘data poor’ areas such as northern Bolivia and the Brazilian province of Acre. A degree of overprediction in the Maxent model (but at probabilities <20%) occurred for some regions where I am confident there were no claylicks (around Iquitos in Peru, in Venezuela, the Brazilian Atlantic Forest and in northern Brazil south of Guyana and Suriname, Figure 2.2).

I am less sure that we know about all the parrot species that use claylicks. Parrot species richness increases with observer effort and few claylicks have been the subject of ongoing investigations. Parrot species with ranges in southwest Amazon, such as Green-cheeked Parakeet *Pyrrhura molinae*, may engage in geophagy unreported as of yet.

### 2.5.2 Characteristics of the parrot community that use claylicks

The analyses showed that parrot claylicks are strongly associated with tropical forest areas. Community analysis indicated that claylick parrot assemblages are largely similar within the core zone of claylick distribution. In turn, tropical forest parrots appear to have a greater need to engage in geophagy than communities associated with savanna or other biomes where no parrots have been reported using mammalian geophagy sites, for example, in the Pantanal, Brazil (de Oliveira et al., 2006).

Life history characteristics were poor correlates of claylick use among parrots. Although Diamond (1999) reported a trend towards larger species of birds eating clay in New Guinea, median parrot weight was not significantly higher for South America claylick users compared to non-users and correlative analyses on traits such as body size are likely confounded by phylogenetic relatedness. The lack of strong life history correlates of claylick usage among parrots coupled with the strong spatial autocorrelation among parrot communities using claylicks may indicate a general need for geophagy among the group as a whole within specific regions rather than a requirement by some species across larger geographical areas. For instance, the large *Ara* spp, although found across the continent, consume soil nowhere else in their range except in southeast Peru, where they are joined by a host of other species. This indicates that the drive to consume soil may be more a product of a general dietary deficit across the group, rather than a specific need for detoxification which is more likely to be species-specific as diets differ widely across parrot species within a given area (Ragusa-Netto, 2007, Matuzak et al., 2008).

### 2.5.3 Conditions needed for claylick formation

The presence of soils suitable for geophagy requires the deposition and subsequent exposure of clays, such as smectites, which retain sodium and bind toxins (Levy et al., 1998), so the white sand deposits from Suriname and around Iquitos would be unsuitable for parrot geophagy. Geophagy sites were strongly correlated with basins and younger geological types in the western Amazon, which are regarded as eutrophic compared to northern, central and southern Amazon (Tuomisto, 2007). Geophagy is rare on the Guiana and Brazilian shields, whose soils are mostly nutrient poor (Stark, 1970, Haridasan, 2001). However, sediments of the lower Amazon River have a high content of smectites (Guyota et al., 2007). Smectites are also found in Paraiba (Rodrigues, 2003) and Para, Brazil (Guerra et al., 2006) and other regions where no parrot geophagy is reported.

Depositions of suitable sediments need to be exposed and visible to parrots in order to be found and consumed. Geophagy is not observed along the course of the Amazon River from Iquitos, Peru, to beyond Manaus, Brazil, where the flooding regimes of igapo and várzea forests inundate suitable soils (Worbes, 1985). In contrast, southeast Peru, where the highest number of claylicks is reported, is characterized by tectonic uplift and downcutting rivers that expose large expanses of river bank (Puhakka et al., 1992). These continue to be exposed during the wet season when visitation rates by macaws and large parrots are at their highest (Brightsmith, 2004).

### 2.5.4 What drives geophagy among Neotropical parrots?

Claylick soils are known to have properties that could provide protection against alkaloid toxins, which has led to the theory that parrots consume soil predominantly as a protection from dietary toxins (Gilardi et al., 1999), as parrots consume nutritionally rich but potentially highly toxic foods, especially during the dry season when food is limiting (Terborgh, 1986). However, identifying potentially toxic compounds in seeds is not sufficient to demonstrate toxicity, as toxicity is a dosage- and animal-specific trait

(Janzen et al., 1986). I am unaware of studies which have examined the toxicity of Neotropical parrot diets in this context (Gilardi 1996 tested general toxicity of around X species of parrot food in a brine shrimp bioassay) and none that explore the geographical variation in toxicity. In fact there is limited study of potential toxins in the seeds of most tropical plants. However, seeds from a range of Costa Rican members of the Fabaceae family, identified as an important food family for parrots (Matuzak et al., 2008), contain multiple defensive compounds that can potentially reduce seed predation (Janzen et al., 1986). Some leaves in tropical forests are defended by a wide variety of secondary metabolites (Coley and Barone, 1996) and some of these traits may extend to immature fruit and seeds. In general, better plant defences are associated with plants on poor soils (Janzen, 1974, Coley and Barone, 1996, McKey et al., 1978). If protection from toxins was driving claylick use, we would predict high levels of geophagy in nutrient poor areas such as the Guiana and Brazilian shields (Haridasan, 2001). Instead, parrot claylicks are centred on the nutrient rich deposits at the base of the Andes and I argue that this is not what we would expect if geophagy was driven by the need for protection from dietary toxins. Ultimately, parrots are a family of birds renowned for their ability to deal with ‘toxic’ food sources wherever they are found (Juniper and Parr, 1998).

Due to the physiological importance of sodium to vertebrates (Randall et al., 1997) and its relative scarcity in many ecosystems (Whittaker et al., 1979), the regulation of sodium levels and sodium seeking behaviour are under tight hormonal control (Schulkin, 1991). If sodium deficits are a potential driver of geophagy in this system, one would predict that claylick use would be greatest in areas with the lowest sodium concentrations in the food supply. Claylick use was concentrated in tropical moist forest areas where turnover of sodium is very rapid (Whittaker et al., 1979) and absent from temperate and more arid areas where leaching and weathering are reduced, and sodium concentrations usually higher (Levy et al., 1998).

Claylick use was positively correlated with distance from the ocean. Seasalt aerosol influx in rainfall is an important source of ecosystem sodium, and deposition decreases with distance from the coast. Annual inputs close to the coast can be as high as 65 kg/ha (Heartsill-Scalley et al., 2007) compared to the Amazon average of 3 kg /ha (Mortatti and Probst, 2003). The Andes form a barrier to Pacific rainfall influences to the Amazon basin (Strecker et al., 2007), so oceanic influence is from the eastern sea bodies of the Caribbean and Atlantic Oceans. Geophagy is conspicuously absent from coastal forests such as the Atlantic rainforests and basins of northeast Brazil, and instead is found in the western Amazon where sodium hunger is predicted to be greatest.

The distribution of parrot claylicks across South America has important community and conservation implications for parrot populations. The western Amazon has until now been little impacted by anthropogenic change but now faces increasing infrastructure development with associated conservation implications, including colonisation, deforestation and forest fragmentation. Claylicks in southeast Peru visited by up to 20 parrot species are an anomaly on the gradient of decreasing parrot species richness from northeast to southwest South America (Blackburn et al., 2004). If the presence of geophagy sites aid the persistence of marginalized species in this region remains to be seen, but the impact of increased disturbance on parrot activity at riverside geophagy sites needs to be investigated. The distribution of parrot claylicks across South America lends strength to the theory that the need for sodium results in one of the western Amazon’s most interesting ornithological phenomena, yet much still needs to be understood on the factors, both human and ecological, that influence parrot geophagy across South America.

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Appendix 2.1: Environmental variables considered for use in modelling claylick distribution using Maxent, indicating their original spatial resolution or scale, if they were ultimately used, and the final percent contribution to the model. AVHRR is Advanced Very High Resolution Radiometer; MODIS VCF is MODerate Resolution Imaging Spectroradiometer Vegetation Continuous Field. Bio1 to Bio19 are Bioclim variables (Nix, 1986).

| Environmental variable | Original spatial resolution/ scale | Used (yes/ no) | % Contribution in Maxent model | Data source |
|---|---|---|---|---|
| Elevation | ~1km | Yes | 3.0 | http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html |
| Slope (degrees) | ~1km | Yes | 0.2 | Same as above |
| Northness (cos(aspect)) | ~1km | Yes | 3.3 | Generated from Aspect from http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html |
| Eastness (sin(aspect)) | ~1km | Yes | 0.6 | Generated from Aspect from http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html |
| Compound topographic index | ~1km | Yes | 4.5 | http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html |
| Flow accumulation | ~1km | Yes | - | Same as above |
| Flow direction | ~1km | Yes | 0.1 | Same as above |
| Distance from Pacific and Atlantic oceans | 1km | Yes | 7.2 | Generated in GIS |
| Soil types | 1 x 1 degree | No | - | http://www.sage.wisc.edu/atlas/maps.php |
| Soil pH | 0.5 x 0.5 degree | No | - | Same as above |
| Soil Carbon | 0.5 x 0.5 degree | No | - | Same as above |
| Soil moisture | 0.5 x 0.5 degree | Yes | 2.3 | Same as above |
| Growing degree days | 0.5 x 0.5 degree | No | - | Same as above |
| Evapotranspiration | 0.5 x 0.5 degree | Yes | 1.8 | Same as above |
| Potential Evapotranspiration | 0.5 x 0.5 degree | Yes | 0.0 | Same as above |
| Geology | 1:1 million | No | - | Hearn et al. (2000) |
| Geological age | 1:1 million | No | - | Hearn et al. (2000) |
| AVHRR land use land cover types | 1km | Yes | 20.4 | Hansen et al. (2000); available at http://glcf.umiacs.umd.edu/data/ |
| MODIS VCF- Bare cover | 500 m | Yes | 3.0 | Hansen et al. (2003); available at http://glcf.umiacs.umd.edu/data/ |
| MODIS VCF- Tree | 500 m | Yes | 0.1 | Same as above |

| | | | | |
|---|---|---|---|---|
| cover | | | | |
| MODIS VCF- Herb cover | 500 m | Yes | 4.8 | Same as above |
| Annual mean temperature (Bio1) | ~1km | No | - | Hijmans et al. (2005); available at http://www.worldclim.org/ |
| Mean diurnal range in temperature (Bio2) | ~1km | Yes | 0.0 | Same as above |
| Isothermality (Bio3) | ~1km | Yes | 0.0 | Same as above |
| Temperature seasonality (SD x 100) (Bio4) | ~1km | Yes | 12.1 | Same as above |
| Maximum temperature of warmest month (Bio5) | ~1km | No | - | Same as above |
| Minimum temperature of coldest month (Bio6) | ~1km | No | - | Same as above |
| Temperature annual range (Bio7) | ~1km | Yes | 0.0 | Same as above |
| Mean temperature of wettest quarter (Bio8) | ~1km | No | - | Same as above |
| Mean temperature of driest quarter (Bio9) | ~1km | No | - | Same as above |
| Mean temperature of warmest quarter (Bio10) | ~1km | No | - | Same as above |
| Mean temperature of coldest quarter (Bio11) | ~1km | No | - | Same as above |
| Mean annual precipitation (Bio12) | ~1km | Yes | 0.2 | Same as above |
| Precipitation of wettest month (Bio13) | ~1km | No | - | Same as above |
| Precipitation of driest month (Bio14) | ~1km | Yes | 3.2 | Same as above |
| Precipitation seasonality (CV) (Bio15) | ~1km | Yes | 0.6 | Same as above |
| Precipitation of wettest quarter (Bio16) | ~1km | No | - | Same as above |
| Precipitation of driest quarter (Bio17) | ~1km | No | - | Same as above |
| Precipitation of warmest quarter (Bio18) | ~1km | Yes | 31.3 | Same as above |
| Precipitation of coldest quarter (Bio19) | ~1km | Yes | 1.0 | Same as above |

Appendix 2.2: The characteristics of South American parrot species whose range overlaps with at least one of claylick.

| Common Name | Number of licks visited | Number of licks in range | Proportion of licks visited | Range (1000 km$^2$) | Abundance | IUCN ranking | Habitat breadth | Diet breadth | Ave weight (g) | Average ranked abundance on licks | n | Average ranked perceived abundance | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Maroon-bellied Parakeet | 1 | 1 | 1.00 | 1600 | 3 | 5 | 3 | 5 | 88 | 1 | 1 | | |
| Blue-headed Parrot | 19 | 24 | 0.79 | 8300 | 4 | 5 | 5 | 4 | 251 | 2.4 | 18 | 1.8 | 18 |
| Yellow-crowned Parrot | 16 | 24 | 0.67 | 6700 | 3 | 5 | 6 | 2 | 440 | 1.7 | 15 | 1.67 | 15 |
| Peach-fronted Parakeet | 2 | 3 | 0.67 | 5700 | 3 | 5 | 3 | 5 | 86.5 | 2 | 2 | 1 | 2 |
| Red-and-green Macaw | 16 | 25 | 0.64 | 8100 | 3 | 5 | 3 | 2 | 1214 | 1.6 | 16 | 2 | 19 |
| Mealy Parrot | 15 | 24 | 0.63 | 7200 | 3 | 5 | 5 | 3 | 626 | 2.4 | 15 | 2.53 | 15 |
| Dusky-headed Parakeet | 15 | 24 | 0.63 | 2300 | 3 | 5 | 3 | 5 | 108 | 2.3 | 15 | 1.56 | 16 |
| Orange-cheeked Parrot | 13 | 22 | 0.59 | 3500 | 3 | 5 | 1 | 3 | 140 | 1.3 | 12 | 1.08 | 13 |
| Chestnut-fronted Macaw | 14 | 24 | 0.58 | 5800 | 3 | 5 | 2 | 2 | 343 | 2 | 14 | 2 | 18 |
| Cobalt-winged Parakeet | 11 | 20 | 0.55 | 2600 | 3 | 5 | 3 | 3 | 56 | 2.4 | 11 | 2.47 | 15 |
| Military Macaw | 1 | 2 | 0.50 | 298 | 1 | 4 | 3 | 3 | 1134 | 1.5 | 2 | 1.5 | 2 |
| Golden-winged Parakeet | 1 | 2 | 0.50 | 3100 | 3 | 5 | 3 | 4 | 54.5 | | | | |
| White-eyed Parakeet | 12 | 25 | 0.48 | 10000 | 3 | 5 | 4 | 2 | 158 | 1.7 | 12 | 1.8 | 15 |
| Black-capped Parakeet | 6 | 14 | 0.43 | 550 | 3 | 5 | 2 | 3 | 75 | 1.5 | 6 | 2 | 9 |
| Scarlet Macaw | 10 | 24 | 0.42 | 6700 | 3 | 5 | 3 | 3 | 1015 | 1.4 | 10 | 1.69 | 16 |
| Blue-headed Macaw | 6 | 16 | 0.38 | 373 | 2 | 2 | 2 | 2 | 250 | 1.3 | 6 | 1.08 | 12 |
| Crimson-bellied Parakeet | 1 | 3 | 0.33 | 1100 | 3 | 5 | 2 | 2 | 75 | 1 | 1 | 3 | 1 |
| Blue-and-yellow Macaw | 7 | 24 | 0.29 | 7800 | 3 | 5 | 3 | 4 | 1125 | 1.4 | 7 | 1.69 | 16 |
| Amazonian Parrotlet | 4 | 14 | 0.29 | 200 | 1 | 4 | 1 | 2 | 41.5 | 1 | 4 | 1 | 8 |
| White-bellied Parrot | 4 | 19 | 0.21 | 3600 | 3 | 5 | 2 | | 155 | 1 | 4 | 1.83 | 12 |
| Dusky-billed Parrotlet | 4 | 21 | 0.19 | 2900 | 3 | 5 | 2 | 3 | 27.2 | 1 | 4 | 1.18 | 11 |
| Red-bellied Macaw | 4 | 24 | 0.17 | 7200 | 3 | 5 | 4 | 1 | 372 | 1.7 | 3 | 1.38 | 13 |
| Painted Parakeet | 3 | 19 | 0.16 | 4000 | 3 | 5 | 3 | 5 | 62.1 | 1 | 1 | 1.33 | 3 |
| Orange-winged Parrot | 1 | 8 | 0.13 | 7400 | 4 | 5 | 5 | 3 | 370 | 1 | 1 | . | |
| Tui Parakeet | 1 | 19 | 0.05 | 1700 | 4 | 5 | 1 | 2 | 59 | 2 | 1 | 1 | 2 |
| Scarlet-shouldered Parrotlet | 1 | 22 | 0.05 | 1800 | 2 | 5 | 1 | | 60 | 1 | 1 | 1 | 4 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Festive Parrot | 0 | 4 | 0.00 | 860 | 3 | 5 | 4 | | 430 |
| Black-headed Parrot | 0 | 4 | 0.00 | 2900 | 3 | 5 | 2 | 5 | 157 |
| Maroon-tailed Parakeet | 0 | 4 | 0.00 | 1500 | 3 | 5 | 2 | | 67.9 |
| Sapphire-rumped Parrotlet | 0 | 4 | 0.00 | 3800 | 2 | 5 | 2 | 1 | 59.7 |
| Blue-fronted Parrot | 0 | 3 | 0.00 | 4200 | 4 | 5 | 5 | 2 | 451 |
| Red-shouldered Macaw | 0 | 3 | 0.00 | 4300 | 3 | 5 | 5 | 3 | 156 |
| Monk Parakeet | 0 | 3 | 0.00 | 2800 | 3 | 5 | 4 | 5 | 120 |
| Canary-winged Parakeet | 0 | 3 | 0.00 | 3400 | 3 | 5 | 3 | 3 | 74.6 |
| Red-fan Parrot | 0 | 2 | 0.00 | 4300 | 3 | 5 | 1 | 2 | 246 |
| Scarlet-fronted Parakeet | 0 | 2 | 0.00 | 420 | 4 | 5 | 2 | 3 | 194 |
| Blue-crowned Parakeet | 0 | 2 | 0.00 | 2300 | 3 | 5 | 4 | 3 | 171 |
| Green-cheeked Parakeet | 0 | 2 | 0.00 | 680 | 3 | 5 | 5 | | 77.1 |
| Scaly-headed Parrot | 0 | 1 | 0.00 | 4500 | 3 | 5 | 1 | 2 | 293 |
| Yellow-faced Amazon | 0 | 1 | 0.00 | 1500 | 2 | 4 | 2 | 2 | 260 |
| Blue-winged Macaw | 0 | 1 | 0.00 | | 3 | 4 | 3 | | 256 |
| Vinaceous amazon | 0 | 1 | 0.00 | 106 | 1 | 3 | 2 | 3 | 254 |
| Yellow-collared Macaw | 0 | 1 | 0.00 | 600 | 3 | 5 | 5 | 4 | 245 |
| Pileated Parrot | 0 | 1 | 0.00 | 730 | 3 | 5 | 2 | 2 | 119 |
| Grey-hooded Parakeet | 0 | 1 | 0.00 | 600 | 3 | 5 | 3 | 2 | 33.6 |
| Kawall's Parrot | 0 | 1 | 0.00 | 720 | | 5 | 1 | 2 | |

# Chapter 3: Spatial and temporal patterns of geophagy across a community of parrots in southeastern Peru

## 3.1 SUMMARY

While parrot geophagy at riverside claylicks is mostly a phenomenon observed in the western Amazon forests, no information exists on the spatial distribution of the resources along the rivers of the region. An extensive survey of five major river systems was conducted in the southeastern Peruvian department of Madre de Dios, an area known for parrot geophagy. Selected sites were monitored over a three year period to determine temporal patterns of claylick use for the local parrot assemblage. Parrot geophagy sites ranged from 0.05 to 1.1 per kilometre of river. Species richness varied among claylicks, and although all of the parrots of the region were observed on at least one claylick, no single claylick registered all the region's parrots. Species richness, as determined by feather availability at the base of claylicks, increased westwards. The amount of feeding observed on a daily basis varied ten-fold among monitored sites, and feeding may be a function of the 'area of influence' of a claylick – rivers with fewer claylicks probably have a greater 'parrot catchment area'. Both seasonal and diurnal patterns of claylick use were similar for individual species among claylicks, suggesting species specific strategies to feeding that may be influenced by predation. Although the visual spectacle of a claylick would suggest intense usage by parrots, on average only 1% of the potential population within a 10 km radius were observed at the claylick on a daily basis, although for species associated with secondary habitat this value was much higher. Although this study elucidates patterns of claylick distribution and claylick use, much needs to be done to determine how far individuals are travelling to use claylicks.

## 3.2 INTRODUCTION

Avian geophagy, especially by parrots, occurs in a wide area across South America (Chapter 2). Claylick distribution and patterns of species richness at claylicks across South America lends strength to the role of sodium in clay consumption (Chapter 2). Parrots in southeastern Peru target soil with high cation exchange capacity and high sodium content (Gilardi et al., 1999, Brightsmith and Aramburu Munoz-Najar, 2004, Brightsmith et al., 2008). Parrot geophagy in the western Amazon, where hundreds of birds descending to consume soil at exposed riverbanks on an almost daily basis, has been the subject of several investigations as to the physical properties of the soil (Emmons and Stark, 1979, Brightsmith and Aramburu Munoz-Najar, 2004, Brightsmith et al., 2008, Powell et al., 2009), and a behavioural study (Burger and Gochfeld, 2003). No study has attempted to understand the finer-scale spatial distribution of these sites, while temporal trends in activity have been reported from just two sites (Burger and Gochfeld, 2003, Brightsmith, 2004). With southeastern Peru facing massive development with the completion of a highway through the middle of what was one of the Amazon’s best protected areas (Dourojeanni, 2006), it is important to know where these claylicks are in order to quantify their protected status.

In South America, broad patterns suggest that claylick distribution is related to the availability of suitable soils in areas of sodium deficiency (Chapter 2). Understanding the spatial distribution of claylicks may have important consequences for understanding their impacts on parrot movement, distribution, dietary ecology and conservation. Isolated resources such as mineral licks and artificial water holes have been shown to influence landscape use and abundance in mammals (Smit et al., 2007), and claylicks have been attributed to parrot flight direction patterns in southeastern Peru (Ward, 2007). While some non-migratory birds are capable of flying long distances to obtain resources (Lloyd et al., 2000), how far parrots will travel for resources is not so clear. Munn (1992) estimated that Red-and-green Macaws *Ara chloropterus* fly not more than six to seven kilometres upon leaving a lick on the Manu River and stated it was unlikely that macaws visited a claylick nine kilometres away.

Temporal patterns of parrot claylick use are becoming better understood. For a claylick in Manu National Park (in southeastern Peru), Burger and Gochfeld (2003) report three diurnal patterns of claylick use which appear to be species specific: most small parakeets and all parrots use the claylick in the early morning only; large macaws use the claylick in the mid-morning, while Cobalt-winged Parakeets *Brotogeris cyanoptera* use the claylick in the afternoon. Seasonal patterns in soil consumption at a claylick in southeastern Peru have been linked to breeding season for parrot species observed at claylicks (Brightsmith, 2006). Whether these patterns are site specific or apply to a wider area has not been demonstrated.

Understanding relationships between claylicks and local parrot communities has implications for the use of these sites for population monitoring (Lee, 2009a). Sites where parrots congregate regularly to consume soil may provide useful information - as long term monitoring at one site has shown broadly repeating patterns among years (Brightsmith, 2004). But claylicks may be ephemeral resources impacted by changing environments and the impact of humans - abandonment of mineral sites used by Band-tailed Pigeons *Patagioensis fasciata* in western Oregon has been attributed to land use change (Overton et al., 2006). The department of Madre de Dios in southeastern Peru has a fast growing population and is undergoing rapid development (Dourojeanni, 2006, Naughton-Treves, 2004), so there is a real danger the natural phenomenon of hundreds of parrots coming to the ground to consume soil will disappear before we fully understand it. When, where and how claylicks are used by which parrots, has yet to be broadly described at a community level and this chapter addresses these issues.

### 3.2.1 Aims

Determine the spatial distribution of claylicks in relation to habitat proximity; and classify the parrot community of southeastern Peru on the basis of temporal patterns of claylick use and the numbers of parrots visiting them. To achieve these aims I have the following objectives:

1. Map spatial distribution of parrot claylicks and their species richness in a region of lowland Amazon rainforest in relation to floodplain and *tierra-firme* habitat types
2. Identify daily patterns of claylick visitation by parrots
3. Identify seasonal differences in claylick usage by parrots
4. Determine what proportion of the local parrot population use claylicks on a daily basis
5. Broadly classify the parrot assemblage of Tambopata according to their claylick use patterns

## 3.3 METHODS

### 3.3.1 Study Area

The study was conducted in the Madre de Dios department in southeastern Peru, along lowland Amazon rivers which form part the approximately 160,000 km$^2$ Madre de Dios drainage basin (Goulding et al., 2003). Some riverbanks where geophagy occurs have been identified as intertidal alluvial deposits (Räsänen et al., 1987, Räsänen et al., 1995). The clay is characterized by a high cationic exchange capacity (Gilardi et al., 1999) and contain high levels of sodium (Brightsmith and Munoz-Najar, 2004).

### 3.3.2 Spatial patterns of claylick distribution

A rigorous survey for both avian and mammal geophagy sites was led by Gabriella Vigo Trauco of the Tambopata Macaw Project from July to October 2007, covering 1,760 kilometres of five major river systems and streams in the region (for details see Brightsmith et al., 2009). Claylick locations were identified by regular bird activity around exposed sections of clay, beak-marks, or as indicated by local guides and researchers. Parrot claylick locations were plotted using ArcMap 9.2 (ESRI Inc, 2006). The distances between claylicks and the degree of clustering was measured using Nearest Neighbour feature (ArcToolbox). Claylick species richness was based on feathers found at the base of the claylick for claylicks where monitoring of feeding was not conducted. Spatial autocorrelation for claylick species richness was measured using Moran's I feature (ArcToolbox). High/Low Clustering (Getis-Ord General G) was used to measure the degree of clustering for either high values or low species richness values.

To determine 'areas of influence', the total area under consideration was delimited by the departmental border to the south, the Piedras River to the east and the furthest claylicks encountered to the north (12$^{o}$1'S) and west (71$^{o}$23'W). The area of floodplain and *tierra-firme* forests within 3, 5, 10 and 15km radius of each claylick was calculated using the 'Buffer Features' function (Hawth's tools). Habitat information was extracted from the 'sistemas ecologicas Peru Bolivia' data set available from http://atrium.andesamazon.org/metadata_search.php. Overlapping buffers were merged using the Edit toolbar. The area of intersection of the resulting buffers was calculated using the Intersect tool (ArcToolbox).

### 3.3.3 Temporal patterns of claylick use by parrots

Monitoring of birds visiting claylicks was conducted from January 2006 to December 2008 along two river systems – Las Piedras and Tambopata (Figure 3.1). Five claylicks were monitored along the Tambopata River - Explorer's Inn (EI), Colpa Hermosa (Hermosa), Posada Colpita (Blind II), Colpa Colorado (TRC) and a small tributary of the Tambopata: El Gato Creek (Gato). Monitoring on the Las Piedras River was conducted at the Las Piedras Biodiversity Research Station (Piedras). Previous studies focused on geophagy have been conducted at Hermosa and TRC (Brightsmith and Munoz-Najar, 2004, Brightsmith, 2004).

Claylicks were monitored to obtain indices of species richness and clay consumption. The monitoring protocol follows that described by Brightsmith (2004). A summary of the monitoring protocol is as follows: Observers began watching the lick before the birds arrived (approximately at sunrise) until the birds finished their early morning lick use (usually before 08h00), or at claylicks frequented by macaws until whenever birds had left the area or 17h00 at Hermosa and TRC. Observers recorded the time, number, and species of the first birds that landed on the lick. Starting from this point, observers counted all birds on the lick every five minutes. Multiple observers were used for this task over the course of this study due to the length of the study period and wide distribution of study sites. The principal investigators participated in training and monitoring at all sites. Each observer was trained and tested to ensure they could readily distinguish all of the bird species on the lick. Observers were rotated between sites wherever possible to minimise any observer and site bias. No monitoring was conducted on days with rainy mornings, as rain can potentially reduce bird activity to zero (Brightsmith, 2004). Weather was recorded as sun, cloud, rain or fog each five minutes as per Brightsmith (2004). The time of all boats passing the claylicks were recorded.

Three indices of claylick use were calculated for each species. The principal index was the daily feeding index (generally referred to as claylick use here), calculated as the sum of the five minute counts multiplied by five (birdminutes) to represent all the birds for that period, as described by Brightsmith (2004). This daily feeding index was also used to examine correlations among species and claylicks (Spearman's rank correlations). Since this is a composite value that combines length of feeding and group sizes, two secondary indices are measures of these values. The second index was the total number of five minute counts (feeding counts) where birds were observed on the claylick. The third index was based on the highest count on the clay for each day. Furthermore, the ratio of claylick use for the three highest months to three lowest months was calculated as the 'degree of seasonality'. The mean values for each metric across all five Tambopata claylicks were used for Principal Components Analysis correlation (PCA) community analysis (CAP, 2002).

### 3.3.4 Issues related to monitoring claylick complexes

On the Tambopata River the three claylicks EI, Hermosa and Blind II are located within two kilometres of each other and observations of flight patterns suggested extensive movement among these licks suggesting that each was potentially as likely as the other to be used by the local bird community. As a result, these are considered together as a claylick complex. In addition, individual patterns of claylick use could vary dramatically on a monthly basis but this variation was not seen when claylicks were considered together, as birds seem to favour one claylick over another on an almost daily basis (Lee, 2009a). Gato and Piedras also consisted of clusters of at least three claylicks each. As only one claylick of each cluster could be monitored at these sites at any time, seasonal extrapolations cannot be undertaken for these two claylick. Monitoring at Gato was limited by accessibility issues, and was conducted at one site only, while monitoring at the Piedras complex focused on the site where large macaws were observed regularly.

For the claylick complex (EI, Hermosa, Blind II) the summed daily feeding index, used for analysis of temporal trends, was not based on the same day since monitoring was rarely conducted simultaneously, but instead on cumulative days from the same monthly period, i.e. the first day of monitoring at each claylick was summed regardless of date and this process repeated up the maximum number of days monitored at any claylick. So although 885 days were monitored all together across the complex these are condensed into 320 days (monthly means were used to make up for shortfall in monthly monitoring for any individual claylick, and consist of 9% of data). This was also done for the maximum count estimates across the complex (see below).

To present data on seasonal patterns, average daily feeding at each claylick for each month was calculated as a proportion of the month with the largest amount of feeding. This was done to present standardized visitation rates, as monthly patterns using total numbers between claylicks varied greatly. Similarly, diurnal feeding patterns at each claylick were standardised to the hour with the greatest amount of feeding.

### 3.3.5 The proportion of the local parrot population that visits claylicks

Parrot density was estimated across the landscape and for the area around the complex and TRC using transects and Distance sampling techniques in Chapter 4. Briefly, transects of two, three and five kilometres length were conducted from sunrise and in the late afternoon before sunset. Transects were located through representative habitats at each site.

To determine the proportion of birds of a local population that visits the monitored claylicks on a daily basis, the mean highest on clay count for the five Tambopata River claylicks was divided by the regional population estimates for differing distances from the claylick i.e. proportion of population using claylick = (mean high count / (density * $\pi$ * km radius$^2$)).

To examine this pattern in more detail at the site level, at Hermosa, EI and Blind II (the complex) an estimate of the total number of birds present was noted after peak activity had finished; referred to as the maximum count. At TRC the claylick high count was used, as the large numbers of birds observed in the physical area of the claylick combined with anti-predatory flushes resulted in wide variation in estimations of maximum counts by observers. To calculate the proportion of each species' local population that visit on a daily basis, the mean maximum count at the complex and TRC was divided by the population estimates for those sites.

### 3.3.6 Statistical analysis

PCA analysis using Pisces software (CAP, 2002) was used to classify the parrot community based on feeding patterns and habits. Kruskal-Wallis tests were used to compare species richness and daily feeding across claylicks. Measures of similarity (Pearson correlation coefficients) in monthly feeding were calculated based on proportional monthly feeding using the ‘Distances Correlation’ function in SPSS (version 16.0). Mann-Whitney U tests were further used to test differences in proportional feeding, mean daily feeding, feeding counts and mean high count between TRC and the complex. Spearman’s rank correlations were used to test relationships between parrot feeding and claylick physical variables (height, area, open area in front of the claylick); and on indices of feeding and parrot weight.

## 3.4 RESULTS

### 3.4.1 Spatial distribution of parrot claylicks

The locations of 62 claylicks used by parrots were mapped, combining results from the formal river survey (covering 1,760 km) with seven previously identified claylicks. For spatial analysis, the area encompassing these claylicks, plus a buffer of 20 km (a distance deemed sufficient to encompass all claylicks and representative habitats) was calculated (Figure 3.1). This area covered 35,700 km$^2$, of which 5,704 km$^2$ (16%) was floodplain forest and 28,021 km$^2$ (78.5%) was *tierra-firme*. The remaining area – 1,975 km$^2$ (5.5%) - consisted of rivers, roads or anthropogenically modified habitat.

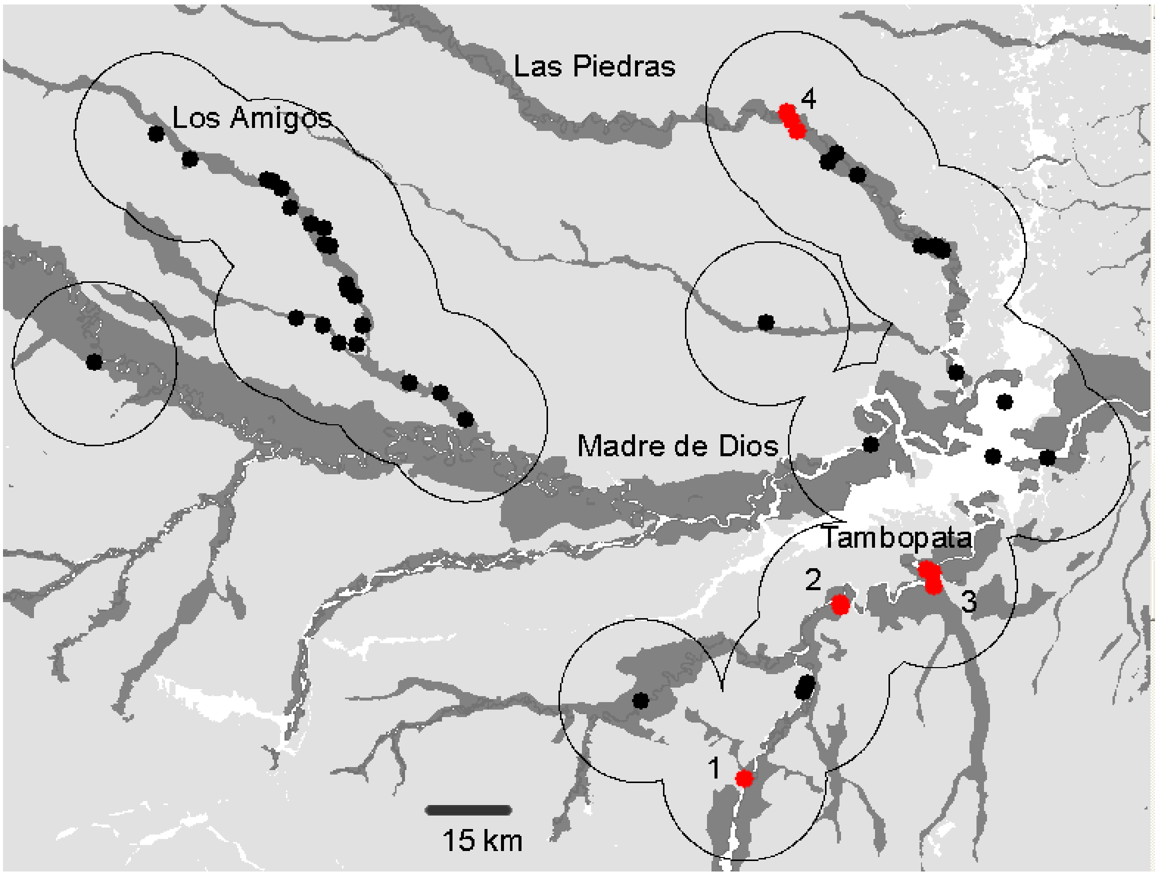

Figure 3.1: A map of the Madre de Dios department of Peru showing surveyed rivers. Light grey fill indicates *tierra-firme* forest, dark grey indicates floodplain forest, white indicates other land types including river edge and anthropogenically modified landscapes. Dots indicate parrot or macaw claylicks. Red dots indicate position of claylicks for which monitoring of bird activity took place: 1 – TRC, 2 – Gato, 3 – Hermosa complex (consisting of the claylicks Hermosa, Blind II and EI), 4 – Piedras. The thin dark line indicates the limit of a 15 km buffer (claylick 'area of influence').

For the 3 km buffer the proportion of each habitat encompassed was roughly equivalent (floodplain: 42% vs *tierra-firme*: 45%), while *tierra-firme* formed a greater proportion of the larger 15 km buffer (floodplain: 23% vs *tierra-firme*: 68%). As a proportion of the total habitat size (amount of habitat in a buffer / total amount of habitat in the area) a greater proportion of floodplain forest was found in proximity to claylicks compared to *tierra-firme* forest (Figure 3.2; 15 km buffer: $\chi^2_1 = 4.3$, $p = 0.04$).

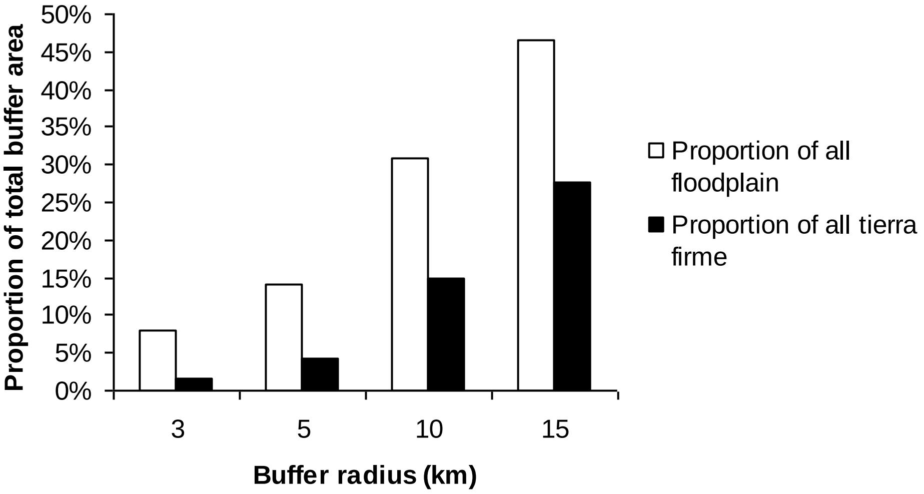

Figure 3.2: The amount of floodplain forest and *tierra-firme* forest as a proportion of the total survey area within combined buffers of 3 – 15 km radius from the nearest claylick.

Mean distance between claylicks was 5.1 km (ranging from 1.8 to 57.9 km). Average nearest neighbour analysis showed a significantly clustered spatial arrangement ($Z = -7.9$, $p < 0.01$), possibly owing to the close association with river features. Claylick density per river (claylicks per tract of river surveyed) was a better measure of claylick abundance as it included start and end sections of surveyed river, which are not accounted for in nearest neighbour analysis. Claylick density was highest on the Piedras (1.1 claylicks per km) and lowest on the Colorado (0.05 per km; Table 3.1). Patterns of claylick distribution in terms of clustering differed between rivers, showing either a more dispersed than expected distribution or random (normal) distribution (Table 3.1).

Table 3.1: Claylick spatial distribution on major rivers of the Madre de Dios department of Peru. Parrot species richness is mean number of parrots ± S.D.

| River | Km formal survey | Claylicks | Claylicks / 10 km tract of river surveyed | Mean nearest neighbour (km) | Parrot species richness |
|---|---|---|---|---|---|
| Tambopata | 110 | 11 | 1.0 | 8.8 | 7.6 ± 5.2 |
| Piedras | 144 | 18 | 1.3 | 3.5 | 3.6 ± 2.4 |
| Amigos | 118 | 14 | 1.2 | 2.8 | 1.4 ± 1.1 |
| Colorado | 91 | 5 | 0.5 | 5.0 | 2.3 ± 3.7 |
| Madre de Dios | 72 | 12 | 1.7 | 10.9 | 4.8 ± 3.5 |

Claylick species richness for 62 identified parrot claylicks ranged from one to 16 (mean: 4.1 ± 3.8; Table 3.1). A degree of spatial autocorrelation with the number of parrot species attributed to each lick was detected (Moran's I = 0.36, Z = 1.88, $p = 0.06$). There was a significant increase in species richness from east to west ($r_s = +0.26$, $p = 0.04$, n = 65), while there was a near significant negative correlation between species richness from north to south ($r_s = -0.24$, $p = 0.06$, n = 65), suggesting the spatial autocorrelation may result from higher species richness to the west. There was no correlation between claylick abundance on a river and claylick species richness on that river ($r_s = -0.1$, $p = 0.8$, n = 5).

### 3.4.2 Temporal patterns of claylick use: survey effort and broad correlations

A total of 1,614 monitoring sessions were conducted at six claylicks (Table 3.2). Claylicks differed both in terms of daily parrot species richness (Kruskal-Wallis: $\chi^2_5 = 824$, $p < 0.001$) and daily feeding (Kruskal-Wallis: $\chi^2_5 = 580$, $p < 0.001$). The largest claylick (TRC) experienced ten times more daily feeding than the smallest (Blind II). Standard deviation was higher than the mean daily feeding for all cases except at TRC and Hermosa, indicating a high degree of variability in daily parrot visitation.

Table 3.2: A summary of claylick characteristics, claylick use by parrots and monitoring conducted at five parrot claylicks on the Tambopata River and a claylick on the Las Piedras River. Species richness and feeding are presented as median, interquartile range (25th – 75th percentiles). For the complex Total Feeding represents the compounded feeding value.

| | Complex | | | | TRC | Gato | Piedras |
|---|---|---|---|---|---|---|---|
| | Blind II | EI | Hermosa | Total | | | |
| Width (m) | 15 | 30 | 400 | | 400 | 80 | 25 |
| Height (m) | 5 | 8 | 6 | | 25 | 10 | 15 |
| Days observation | 275 | 266 | 344 | | 475 | 128 | 126 |
| Species richness | 2, 1-3 | 4, 1-5 | 5, 3-7 | | 9, 7-11 | 2, 1-4 | 2, 1-3 |
| Total # of species | 11 | 11 | 12 | 15 | 16 | 11 | 10 |
| Feeding (birdminutes) | 140, 15-597 | 272, 36-615 | 727, 331-1268 | 1585, 815-2851 | 2880, 1215-5060 | 290, 40-750 | 752, 251-1447 |

The claylick with the highest total species richness was TRC (16 parrot species) while 15 species used one or other of the claylick complex sites, representing 89% and 83% of the parrot species recorded in the study area along transects respectively (n = 18). Species richness was correlated with days monitoring ($r_s = 0.94$, $p = 0.005$, n = 6), while daily feeding was not ($r_s = 0.6$, $p = 0.21$, n = 6). Neither species richness nor daily feeding was correlated with any other physical attribute variables: claylick surface area, open area of river in front of claylick, boat traffic or weather ($r_s < 0.7$, $p > 0.1$, n = 6 for all variables).

### 3.4.3 Community analysis of the parrot assemblage by claylick use patterns

The PCA analysis based on feeding patterns at the six claylicks extracted three eigenvalues >1, which represent 81% of the total variance (Figure 3.3). Values used in the analysis are in Appendix 3.1. Although species' seasonality, group size and the proportion of claylicks used formed the principal components of the axes, there was no temporal pattern or feeding strategy common to all 17 species. There were no groupings by genus, with the four *Ara* spp. spread across the principal axes. The two parrotlet species were closely grouped, feeding at the fewest claylicks, in the smallest group sizes, and least often. Some species that were well represented on single claylicks (e.g.

Blue-and-Yellow Macaw *Ara ararauna* and Red-bellied Macaw *Orthopsittaca manilata)* were not recorded at any other claylick. Only five of the 17 species were well represented and regular at most of the claylicks *(*Red-and-Green Macaw *A. chloropterus*, Mealy Parrot *A. farinosa,* Dusky-headed Parakeet *A. weddellii,*Blue-headed Parrot *P. menstruus,* Cobalt-winged Parakeet *B. cyanoptera).*

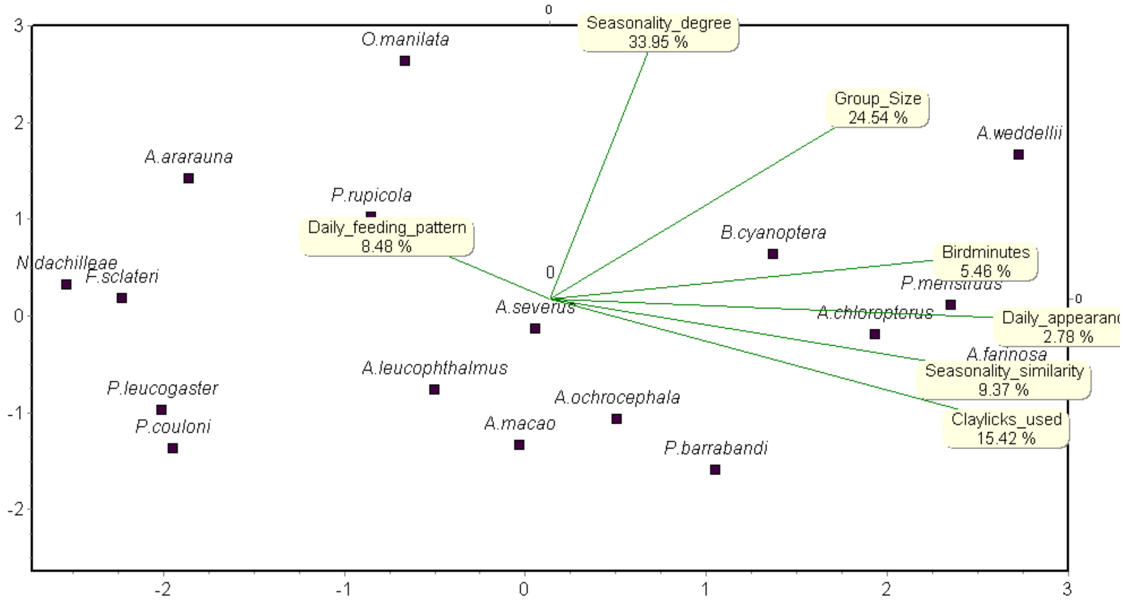

Figure 3.3: A PCA plot (axis 1 vs axis 2) of parrot community structure based on patterns of claylick use for six claylicks across southeastern Peru, with variation accounted for displayed below eigenvectors.

Individual species patterns of claylick use for the complex and TRC, for which we have complete data, are presented in Appendix 3.2. Black-capped Parakeet *Pyrrhura rupicola* was the only species recorded at the complex not recorded at TRC, while Blue-and-Yellow Macaw *A. ararauna* and Red-bellied Macaw *O. manilata* were never observed at the complex. Amazonian Parakeet *Nannopsittaca dachilleae,* Blue-headed Macaw *P.couloni* and White-bellied Parrot *P. leucogaster* used the claylicks on less than 10% of observed days.

At TRC larger species fed on more days (weight vs overall use: $r_s = 0.75$, $p = 0.001$, n = 17); for longer (weight vs feeding counts: $r_s = 0.81$, $p < 0.001$, n = 16) and in the largest groups (weight vs mean high: $r_s = 0.63$, $p = 0.007$, n = 17). Weight was not correlated with these indices for the complex (overall use: $r_s = 0.16$, $p = 0.54$, n = 17; feeding counts: $r_s = -0.12$, $p = 0.68$, n = 17; mean high: $r_s = 0.13$, $p = 0.65$, n = 17), where instead species that fed in larger group sizes fed for longer (correlation feeding counts and mean high complex: $r_s = 0.67$, $p = 0.006$, n = 15; TRC: $r_s = 0.49$, $p = 0.06$, n = 16;).

### 3.4.4 Seasonal patterns of claylick use

The degree of seasonality (ratio of claylick use for the three highest months to three lowest months) contributed 34% of variability to the main axis of the PCA, and species values are presented in Appendix 3.1. The highest score (representing least change between seasons) was Red-bellied Macaw *O. manilata* (0.3), while the species with the lowest scores (greatest seasonality) were Blue-headed Macaw *P. couloni* (0.02) and White-bellied Parrot *P. leucogaster* (0.04). Eight species of 11 that were recorded feeding at multiple claylicks, show similar monthly feeding patterns among the Tambopata claylicks (Pearson's similarity coefficients >60% - Figure 3.4). There was no correlation between parrot weight and the between lick similarity coefficients ($r = 0.33$, $p = 0.33$, n = 11). The mean of the coefficients for 15 parrot species was 0.15 ± 0.08, suggesting a fairly consistent pattern of variability for the assemblage.

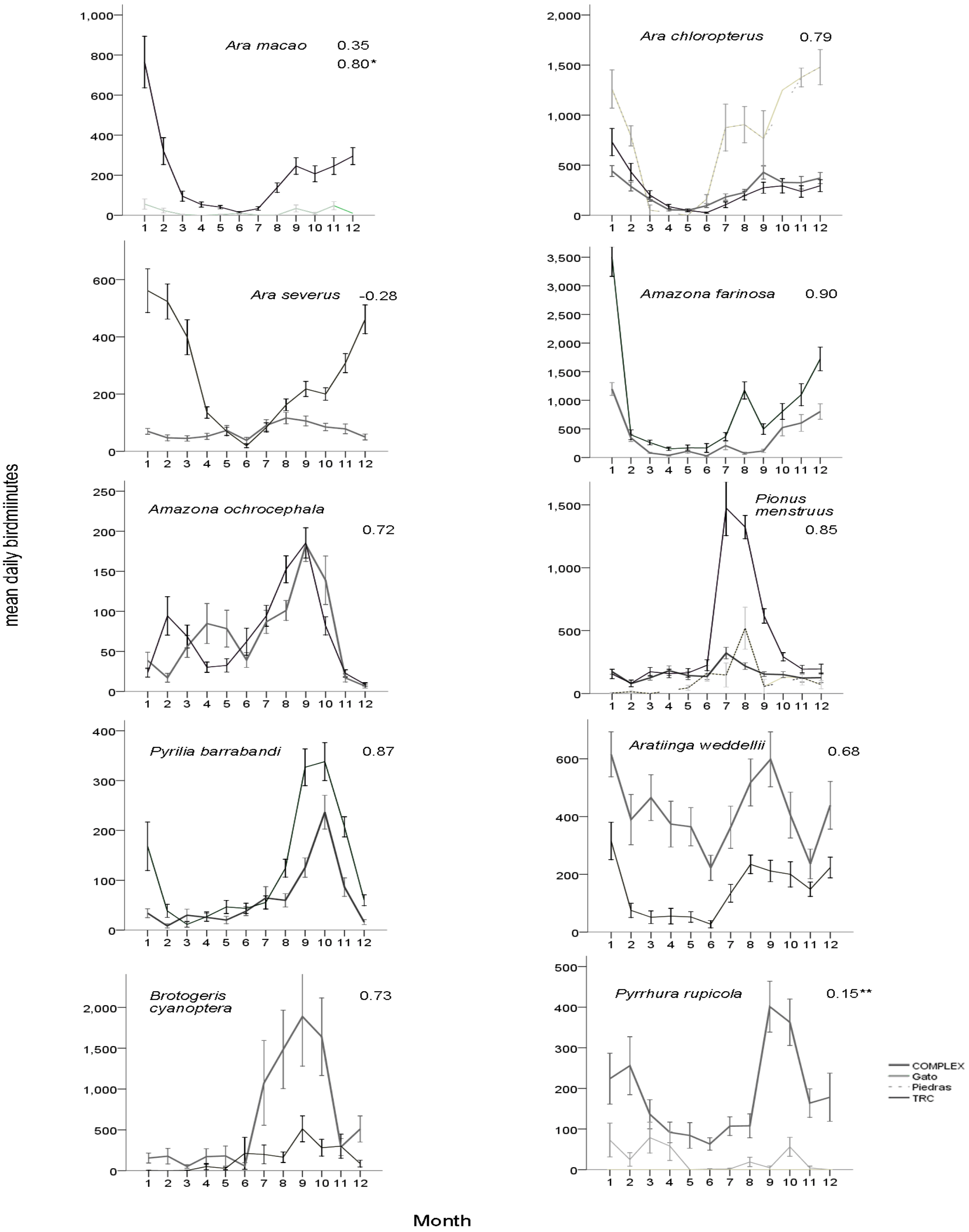

Figure 3.4: Daily claylick use for ten parrot species showing monthly variation for claylicks with sufficient data. In-chart values indicate the distance similarity coefficient. Values close to 1 indicate strong positive correlation of feeding between claylicks, 0 indicates no correlation, -1 indicates negative correlation. * - correlation between Gato and TRC, ** Gato and Complex. Error bars represent standard error.

### 3.4.5 Diurnal patterns of claylick visitation by parrots

Daily feeding strategies could be divided into two broad groups: one group where 95% of feeding occurred before 08h00, and the rest where less than 50% of feeding occurred during this time period, but which instead usually fed from mid-morning onwards (Figure 3.5). The ‘early morning’ group consisted of the following ten species: Yellow-crowned Parrot *A. ochrocephala,* Mealy Parrot *A. farinosa,* Red-bellied Macaw *O. manilata,* Blue-headed Parrot *P. menstruus,* White-eyed Parakeet *A. leucophthalma,* Orange-cheeked Parrot *P. barrabandi,* Dusky-headed Parakeet *A. weddellii,* White-bellied Parrot *P. leucogaster* and Blue-headed Macaw *P. couloni*. The species that feed at any time of the day include: Blue-and-yellow Macaw *A. ararauna*, Cobalt-winged Parakeet *B. cyanoptera*, Black-capped Parakeet *P. rupicola,* Scarlet Macaw *A. macao,* Red-and-green Macaw *A. chloropterus* and Amazonian Parrotlet *N. dachilleae*. Of the later group, *Ara* spp fed mostly mid-morning, while Cobalt-winged Parakeet *B. cyanoptera* fed mostly in the afternoon. Similarities among sites, based on hourly feeding, were highest for species that fed in the early morning, and lowest for the late morning feeders Scarlet Macaw *A. macao* and Red-and-Green Macaw *A. chloropterus*. Daily feeding trends for Red-and-Green Macaw *A. chloropterus* and Scarlet Macaw *A. macao* were more similar between species for individual sites than for the same species at different sites as these species often fed together.

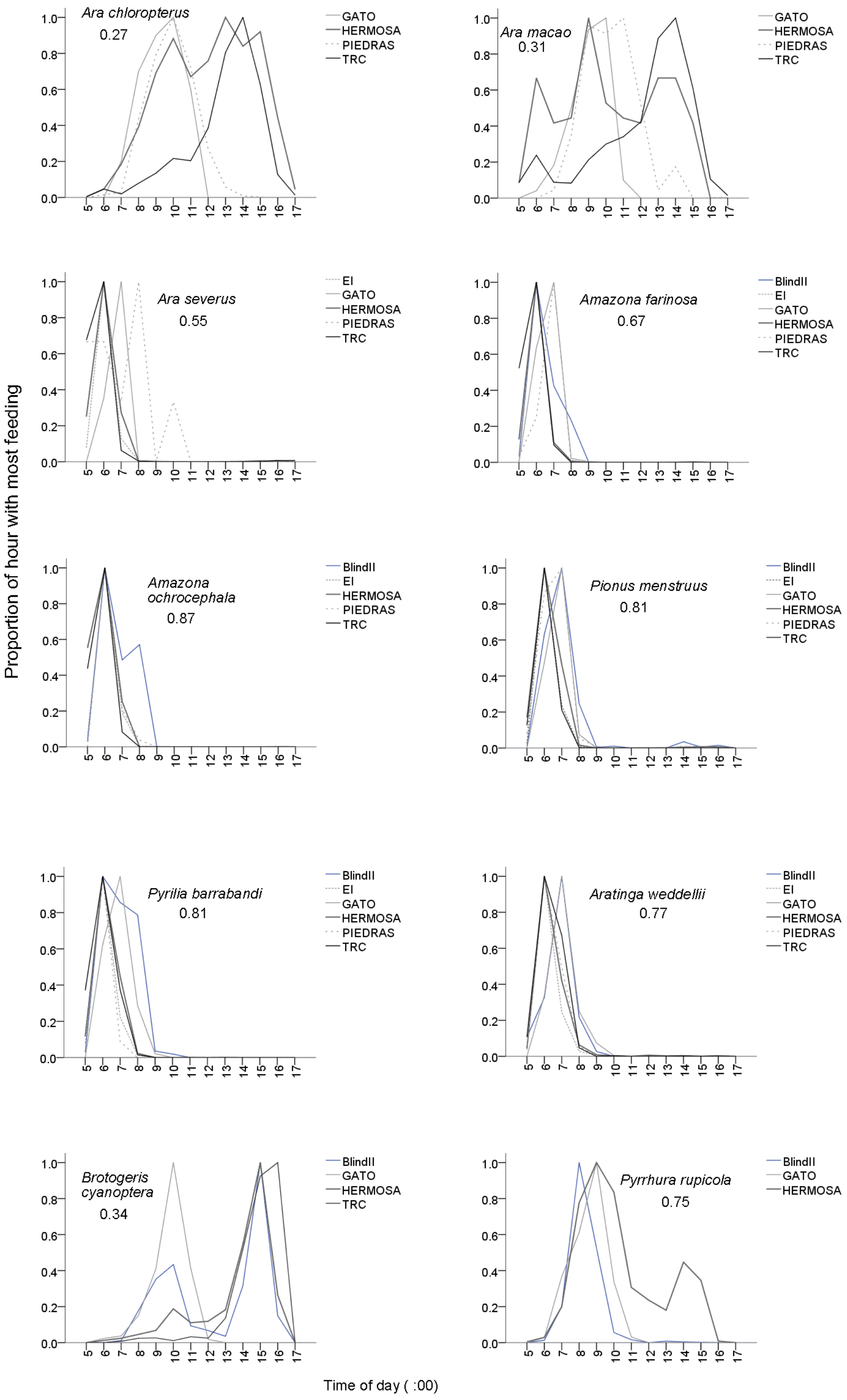

Figure 3.5: Feeding time (standardized to a proportion of the interval with most feeding) for ten parrot species that fed at more than one site. Values below species names represent mean Pearson's similarity coefficients for all sites.

### 3.4.6 The proportion of parrots that use claylicks

The proportion of the local parrot population using claylicks varied widely (Figure 3.6; Table 3.3). Visitation rates were lowest for Black-capped Parakeet *P. rupicola* and White-bellied Parrot *P. leucogaster,* represented by the lowest proportion of birds at the claylick as a proportion of the population. The species represented on the claylick as a high proportion in relation to density were Chestnut-fronted Macaw *A. severus,* Dusky-headed Parakeet *A. weddellii* and White-eyed Parakeet *A. leucophthalma* – all species associated with secondary forests. For the densities used to account for the mean claylick high counts, all Dusky-headed Parakeet *A. weddelli* would have had to have come from a 150 km$^2$ area, Chestnut-fronted Macaw *A .severus* from 110 km$^2$, and White-eyed Parakeet *A.leucophthmalma* and Yellow-crowned Parrot *A. ochrocephala* from 30 km$^2$.

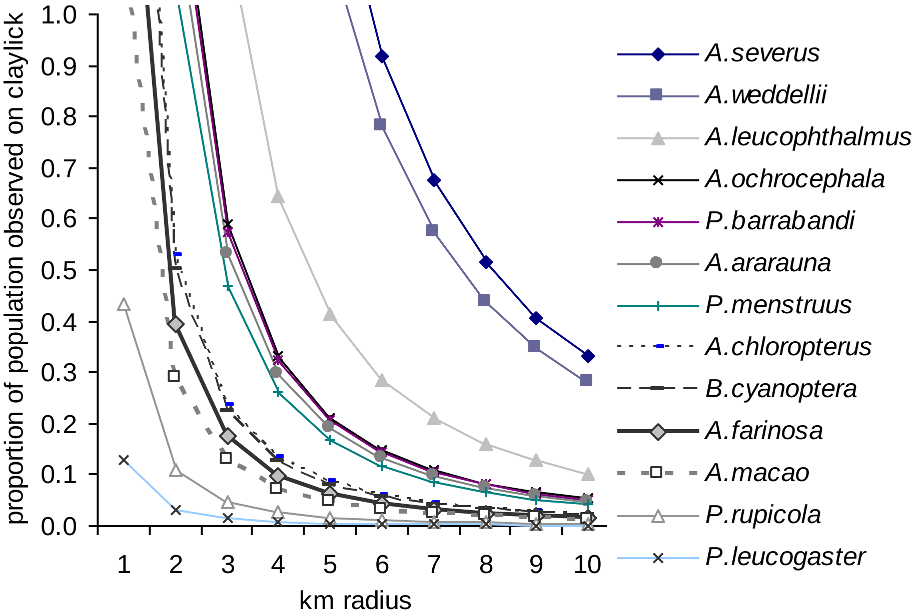

Figure 3.6: The proportion of the population that could be feeding on the claylick for 12 species of parrot in relation to increasing distance from a claylick. Proportion values are based on regional population estimates (Chapter 4) and the mean maximum number of birds for five claylicks.

Less than 10% of the parrots within a 10 km radius of either TRC or the claylick complex fed on a daily basis overall, with most species represented by less than 1% (Table 3.3). At both sites the species represented most as a proportion of local density on the claylicks were Chestnut-fronted Macaw *A. severus* and Dusky-headed Parakeet *A. weddellii.* At the complex there was a significant correlation between claylick use and local density ($r_s = 0.66$, $p = 0.03$, n = 11). At TRC this correlation was weaker ($r_s = 0.57$, $p = 0.07$, n = 11). More abundant species were seen at the claylick on a greater proportion of days at TRC than rare species ($r_s = 0.8$, $p = 0.003$, n = 11).

Table 3.3: Parrot population within 10 km radius of the claylicks (N), mean maximum counts of birds in the area of the claylick for the complex and highest on-claylick counts for TRC (claylick), and the proportion of N represented by the highest counts (claylick/N).

| | Complex | | | TRC | | |
|---|---|---|---|---|---|---|
| Species | N | claylick | claylick/N | N | claylick | claylick/N |
| Dusky-headed Parakeet | 207 | 94±35 | 45.3% | 207 | 23 | 10.8% |
| Chestnut-fronted Macaw | 57 | 19±10 | 33.9% | 57 | 18 | 31.9% |
| White-eyed Parakeet | 138 | 13±17 | 9.7% | 480 | 49 | 10.1% |
| Yellow-crowned Parrot | 283 | 25±18 | 8.9% | 88 | 9 | 10.5% |
| Orange-cheeked Parrot | 283 | 20±12 | 7.0% | 1225 | 13 | 1.0% |
| Blue-headed Parrot | 1256 | 43±18 | 3.4% | 2305 | 32 | 1.4% |
| Mealy Parrot | 3564 | 96±71 | 2.7% | 5432 | 49 | 0.9% |
| Cobalt-winged Parakeet | 4481 | 96±78 | 2.1% | 575 | 50 | 8.6% |
| Red-and-green Macaw | 955 | 14±9 | 1.5% | 1118 | 15 | 1.3% |
| Scarlet Macaw | 314 | 3±3 | 1.0% | 3847 | 10 | 0.2% |
| Black-capped Parakeet | 3347 | 22±9.8 | 0.7% | 0 | 0 | |
| White-bellied Parrot | 3454 | 4±2 | 0.1% | 1134 | 5 | 0.5% |
| Blue-and-yellow Macaw | 66 | 0 | 0.0% | 1130 | 11 | 1.0% |

## 3.5 DISCUSSION

### 3.5.1 Claylick spatial distribution

Claylicks were common along all the river edges surveyed in southeastern Peru and there is no reason that rivers that were not surveyed in the region will not also likewise have at least a parrot claylick per 5 to 10 km tract of river, anthropogenic disturbance aside. A greater proportion of floodplain forest occurs within 15 km radius of a claylick compared to *tierra-firme* forest, so claylicks are thus easily accessible for parrots within floodplain forest types. Whether parrots of *tierra-firme* areas survive long periods without clay, travel longer distances to visit claylicks, or whether they instead use claylicks of the forest interior or alternative resources is still unclear. Several parrot species were observed feeding on termitaria during this study, and a wide variety of primates have been observed feeding on termitaria across the Amazon (Ferrari et al., 2008).

A surprising result of this study was the very low proportion of the potential local population that are observed at known claylicks on a daily basis overall, given the apparently large numbers of birds that can be seen in the area. Radio-collared Mealy Parrots *Amazona farinosa* visit claylicks around once every four days (*fide* G. Powell, 2009). My study would suggest that individuals of most species would not visit more than this if coming in from >5km away, although individuals probably vary widely in their visitation rates based on their general proximity to claylicks, their physical condition and consequent need to visit the claylick, dietary patterns and breeding status. Few of these variables could be quantified during this study.

Whether species associated with secondary habitats use claylicks more based simply on resource proximity, or on dietary deficiencies is still a matter of speculation. The role of claylick dependence in relation to diet is further discussed in Chapter 5. Successional forest makes up a small proportion (<5%) of the total habitat types in the area considered here, but species preferring successional forest can be very abundant within this habitat type (Cowen, 2008) although they appeared relatively uncommon over the wider landscape. The apparent large areas from which the local population would need to be recruited to account for the numbers observed on the claylicks are most likely an overestimate given that regional density estimates were used that encompass a range of habitat types. However, since successional forest tends to be a linear habitat following the course of rivers, successional forest specialists would still need to travel the furthest and/or most regularly in order to account for the larger numbers of birds seen on the claylick.

From facial photographs Munn (1992) determined that individuals were revisiting the observed claylick every second to third day and estimated that the lick was used by between 250 and 350 individual macaws by identifying individuals based on unique feathering patterns. If this is the case and macaw abundance is 2 per km$^2$ (Chapter 4, Terborgh et al., 1990) then the 'catchment area' for that lick was around 150 km$^2$, i.e. the claylick had an approximate radius of 7 km. Since distances between claylicks ranges from 2 to 10 for the five rivers surveyed there is probably little need to travel more than these distances. Blue-and-Yellow Macaws *Ara ararauna* with satellite collars seasonally range up to 150 km from claylicks (Brightsmith unpublished data.)

and Red-bellied Macaws *O. manilata* visit TRC from a palm swamp 13 km away, so claylick influence is likely species and site dependent. Use of the series of claylicks situated only a few kilometres apart suggest that parrots can be flexible in their claylick choice over the medium scale as they were willing to travel several kilometres back and forth in order to select a site that best suited their needs. With terrestrial mammals, White-tailed Deer *Odocoileus virginianus* showed no increase in density around licks and travelled several kilometres to visit licks (Wiles and Weeks, 1986), while Lowland Tapir *Tapirus terrestrus* travelled up to 10 km from clearly defined home ranges to visit licks (Tobler, 2008).

Although all parrot species recorded in southeastern Peru were recorded feeding on at least one claylick, no claylick was used by all members of the parrot community, with some species showing strong site affiliation. Claylicks with a large surface area generally attract more parrot species (Chapter 2), while site specific features, e.g. vegetation cover, impact the vertebrate assemblage as a whole (Brightsmith et al., 2009). Species richness from single site surveys indicated uneven patterns of species use as species richness increased westwards. Two environmental gradients may explain the longitudinal change in claylick species richness from east to west: firstly, parrot species richness was higher in the northwest. Rose-fronted Parakeet/Painted Parakeet *Pyrrhura roseifrons* (*picta*) and Tui Parakeet *Brotogeris sanctithomae* occur frequently in that area (Gilardi and Munn, 1998, Terborgh et al., 1990), but were never recorded along the Tambopata or Piedras rivers during the three year census period. Secondly, anthropogenic influence and resulting disturbance and habitat modification increases eastwards, with the areas largest town Puerto Maldonado located towards the east of the department, along with the Interoceanic highway connecting this town to Brazil.

Total feeding at the isolated claylick at TRC was greater than at the claylick complexes. Difference in parrot abundance does not explain relative use between the sites, which is much higher at TRC in relation to local parrot densities (Chapter 4). Since parrots feed in groups, a critical group size needed for birds to feel secure and descend to the clay may not be reached if birds are spread between sites and birds that feed in the early morning only may lose the window of feeding opportunity if they travel between claylicks. As TRC is an isolated claylick with nearest neighbour claylicks greater than the mean for the region, the catchment area is probably greater (birds over a wider area have no choice but to visit this claylick), while for communities offered a choice of claylicks, not only will use at any individual lick be lower, but the chances of the minimum number of birds being recruited in order to start feeding will be lower.

### 3.5.2 Temporal patterns of claylick use

The parrot community showed great variation in terms of how many claylicks are visited, seasonal patterns, group sizes and rates of visitation. Within the parrot assemblage there were no clear species groupings based on claylick use in the PCA analysis, suggesting against any phylogenetic basis for claylick use or claylick use strategies. Seasonal trends followed similar patterns for most species, except those associated with secondary forest types - the *Aratinga* species, Cobalt-winged Parakeet *B. cyanoptera* and Chestnut-fronted Macaw *A. severus*. These species are all commonly associated with disturbed or secondary habitats (Chapter 5, Juniper and Parr, 1998). Seasonal trends at the TRC claylick have been commented on before (Brightsmith 2004) and are most likely related to the species breeding season for species where the pattern repeats annually as chicks are regularly fed clay in their diet (Brightsmith et al., 2010). Since the seasonal patterns, like the diurnal patterns, are observed at multiple claylicks across the region, these are evidently also species-specific trends mediated by factors such as food availability, diet, and nesting. Since there is dietary partitioning in this parrot community (Chapter 5), differing seasonal patterns of food availability may influence breeding season, and subsequently claylick use (see Brightsmith, 2006).

Three key diurnal periods for claylick use were identified in this study: early morning for most parakeets and all parrots, late morning for large macaws, and the afternoon period for Cobalt-winged Parakeet *Brotogeris cyanoptera*. These temporal patterns have been observed previously by Burger and Gochfeld (2003) at a claylick on the Manu (c.150 km NW of the Tambopata Research Centre), suggesting diurnal trends in claylick use are species specific and apply to the region, and are not mediated purely by local claylick physical or environmental characteristics. Although aggression increases with increasing group sizes (Shaw, 2008, Burger and Gochfeld, 2003), most of this aggression is intra-specific and does not suggest that space is a greatly limiting factor leading to the different feeding strategies. Parrots preferred to feed together and would often leave large areas of the clay unoccupied.

Alternate explanations to could explain peaks in early morning activity at the claylick include voiding during the night leading to extreme hunger in the morning. However, if this is the case then I would not predict that the birds would choose clay over other available food choices on which to feed, as disturbance at claylicks, both natural and anthropogenic, means there is a lesser chance of ingestion compared to the targeting of previously identified foraging trees (Chapter 4 – over 30% of foraging encounters with parrots on food trees were repeats i.e. birds were spatially aware of available food items). Since food availability was never less than 10%, either with fruit or flower availability, and that claylick use was not correlated with periods of lowest food availability, would indicate that it is unlikely that birds eat clay simply to satiate hunger pangs in the early morning. In addition, Houston et al. (1988) suggest one would not expect the energy budgets of small birds to be so closely balanced that they need to forage for calories immediately in the morning. Although early morning activity is observed in nectarivores in the early morning under sometimes energetically unfavourable conditions, this behaviour is determined by a limited resource that needs to be accessed early (Timewell and MacNally, 2004). In contrast, clay is available for consumption at all times. When nectarivores change their feeding habits to insectivory, then they adapt their feeding times to correspond with peaks in insect activity (Timewell and MacNally, 2004). Increases in early morning activity have been observed as ‘migratory restlessness’ in Yellow-faced Honeyeaters Lichenostomus chrysops, a seasonal diurnal migrant (Munro and Munro, 1998). Since increased claylick activity is associated with breeding season, when birds should be close to sedentary, this has little bearing on early morning activity patterns.

Instead, diurnal claylick use patterns may reflect four predator evasion strategies. Successful attacks on parrots and parakeets by Collared Forest-falcon *Micrastur semitorquatus*, Ocelot *Leopardus pardalis* and Ornate Hawk-eagle *Spizaetus ornatus* were recorded at Blind II and unsuccessful attacks have been observed at Piedras by the aerial pursuit raptor the Orange-breasted Falcon *Falco deiroleucus*. Predation may thus explain the low species richness for this small claylick located off the main river, compared to other claylicks where predation events and attempts were rarely observed. With respect to diurnal strategies, it thus appears to be that all parrots and most parakeets feed early to avoid avian raptor activity (Cade, 1965, Jaksić, 1982, Roth, 2007). Secondly, large macaws which have relatively fewer avian predators feed later, where they also appear to use the area around the claylick as a social staging ground (Lee, 2009b); thirdly, Cobalt-winged Parakeet *Brotogeris cyanoptera*, which was the areas most common parakeet (Chapter 4), fed in the largest, noisiest groups and thus may rely more on protection from its own numbers than in a temporal feeding strategy aligned with other species. Lastly, Black-capped Parakeet *Pyrrhura rupicola*, which also fed later in the day, was quiet, fed in small groups concealed behind vegetation and hence appears to rely more on camouflage and stealth as a predator evasion technique. This may also explain why this widespread species fed on all but the largest claylick, which was the most exposed of the claylicks. Diamond et al. (1999) also speculated that bird nervousness and patterns of early morning feeding observed at a geophagy site in Papua New Guinea were due to the need to avoid predators.

How far and how often birds travel to visit claylicks has yet to be quantified, however this study and deductions from previous studies would suggest that there is little need to travel more than 10 km on a daily basis for most species of parrots in southeastern Peru due to the abundance of claylicks across the landscape. Species which use *tierra-firme* habitats would often need to travel further, but it was the species associated with successional forests which were best represented at the claylicks. Claylicks characterized by their species assemblage are a unique combination of local species composition and abundance, as well as claylick physical features. Temporal patterns of claylick use should be of use to tourist companies in order to maximise viewing opportunities for tourists. Guidelines for appropriate tourist enterprise behaviour are addressed in Chapter 6.

### 3.5.3 Acknowledgements

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Appendix 3.1: Table with claylick feeding related values used in PCA-correlation analysis. Values represent mean values for six claylicks. Daily appearance was the proportion of days a species was present at a claylick; birdminutes was the mean daily sum of five minute counts on the claylick; group size was the mean number of birds recorded during five minute counts when the species was present; seasonality degree was the mean daily feeding for the three lowest consecutive months as a proportion of feeding for the three highest consecutive months; claylicks used was the proportion of the six claylicks that were used; daily feeding patterns was scored as 1 for species feeding mostly before 8am and 2 for species recorded feeding mostly after 8am; seasonality similarity was the score among claylicks based on monthly similarity (Pearson's coefficient of similarity).

| Species | Days seen (%) | Birdminutes | Group Size | Seasonality degree | Claylicks used | Daily feeding pattern | Seasonality similarity |
|---|---|---|---|---|---|---|---|
| Amazonian Parrotlet | 0.2% | 0.1 | 3.3 | 0.155 | 0.333 | 2 | 0 |
| Black-capped Parakeet | 17.7% | 32.5 | 7.0 | 0.269 | 0.667 | 2 | 0.15 |
| Blue-headed Macaw | 4.7% | 4.3 | 3.7 | 0.02 | 0.5 | 1 | 0 |
| Blue-headed Parrot | 48.3% | 109.9 | 13.8 | 0.249 | 1 | 1 | 0.85 |
| Blue-and-yellow Macaw | 13.0% | 34.9 | 10.7 | 0.223 | 0.167 | 2 | 0 |
| Chestnut-fronted Macaw | 33.9% | 48.8 | 6.6 | 0.202 | 1 | 1 | -0.28 |
| Cobalt-winged Parakeet | 16.6% | 174.7 | 32.3 | 0.125 | 0.833 | 2 | 0.73 |
| Dusky-billed Parrotlet | 0.8% | 1.2 | 4.2 | 0.155 | 0.5 | 2 | 0 |
| Dusky-headed Parakeet | 42.5% | 85.0 | 48.5 | 0.256 | 1 | 1 | 0.68 |
| Mealy Parrot | 42.3% | 179.4 | 19.8 | 0.121 | 1 | 1 | 0.9 |
| Orange-cheeked Parrot | 34.5% | 35.6 | 6.5 | 0.097 | 1 | 1 | 0.87 |
| Red-bellied Macaw | 14.1% | 72.1 | 29.4 | 0.309 | 0.167 | 1 | 0 |
| Red-and-green Macaw | 41.6% | 206.0 | 11.5 | 0.137 | 0.833 | 2 | 0.79 |
| Scarlet Macaw | 23.5% | 38.0 | 4.0 | 0.068 | 0.833 | 2 | 0.8 |
| White-bellied Parrot | 8.9% | 6.1 | 4.0 | 0.045 | 0.333 | 1 | 0 |
| White-eyed Parakeet | 11.9% | 86.5 | 11.8 | 0.074 | 0.833 | 1 | -0.1 |
| Yellow-crowned Parrot | 31.6% | 24.4 | 5.8 | 0.133 | 0.833 | 1 | 0.72 |

Appendix 3.2: Four measures of feeding patterns for 17 species of parrot at the complex and TRC indicating: proportion of days on which feeding was recorded (Overall use), mean daily feeding measured in bird minutes (Birdminutes), mean daily count of 5 minute feeding counts (Feeding counts), the mean of the highest daily 5 minute count (Mean high). P values for Feeding counts and Mean high are presented for species feeding with Overall use >0.010 for both Complex and TRC. Feeding counts and Mean high were based on individual claylick data for the complex. * = p < 0.001.

|  | Overall use |  | Birdminutes |  |  | Feeding counts |  |  | Mean high |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Complex | TRC | Complex | TRC | P | Complex | TRC | p | Complex | TRC | p |
| Amazonian parrotlet | 0.2% | 0.6% | 0.1±1 | 0.4±6 | 0.16 | 4.5±2.1 | 1.7±0.6 |  | 1.5±0.7 | 6.3±3.8 |  |
| Black-capped Parakeet | 72.5% | 0.0% | 177.9±252 | 0 | * | 8.9±11.8 |  |  | 8.8±7.0 |  |  |
| Blue-headed Macaw | 0.6% | 27.2% | 0.1±1 | 25.6±101 | * | 2.0±1.4 | 2.7±2.3 |  | 1.0±0.0 | 3.0±2.2 |  |
| Blue-headed Parrot | 92.5% | 79.8% | 162.5±162 | 433.0±683 | * | 4.1±2.6 | 6.4±3.7 | * | 10.2±8.9 | 32.1±32.4 | * |
| Blue-and-yellow Macaw | 0.0% | 78.1% | 0 | 209.7±258 | * |  | 9.7±7.6 |  |  | 11.1±7.7 |  |
| Chest.-fronted Macaw | 81.6% | 88.4% | 70.7±78 | 262.4±303 | * | 3.3±1.9 | 6.5±3.6 | * | 6.4±5.1 | 18.2±17.5 | * |
| Cobalt-winged Parakeet | 47.8% | 17.3% | 638.2±1746 | 155.0±620 | * | 8.2±6.6 | 4.5±3.8 | * | 39.3±60.4 | 49.8±51.7 | 0.015 |
| Dusky-billed Parrotlet | 0.1% | 0.4% | 0.1±1 | 0.1±1 | 0.25 | 3.0±2.0 | 1.5±0.7 |  | 1.0±0 | 1.5±0.7 |  |
| Dusky-headed Parakeet | 92.2% | 56.4% | 417.8±404 | 144.4±225 | * | 4.5±2.9 | 3.6±2.2 | * | 25.1±20.0 | 22.6±17.7 | 0.331 |
| Mealy Parrot | 81.9% | 84.8% | 332.0±535 | 842.3±1272 | * | 3.9±2.7 | 7.0±3.9 | * | 18.4±24.4 | 49.0±60.6 | * |
| Orange-cheeked Parrot | 76.3% | 66.5% | 60.5±99 | 122.4±183 | 0.006 | 3.4±2.6 | 5.5±3.4 | * | 5.7±5.7 | 12.7±11.2 | * |
| Red-bellied Macaw | 0.0% | 84.4% | 0 | 432.8±568 | * |  | 6.0±3.5 |  |  | 31.5±27.2 |  |
| Red-and-green Macaw | 88.4% | 58.7% | 243.4±246 | 293.3±377 | 0.51 | 13.1±9.7 | 10.1±9.1 | * | 8.1±5.2 | 14.8±11.4 | * |
| Scarlet Macaw | 14.7% | 77.7% | 3.0±9 | 203.1±356 | * | 2.9±2.0 | 8.9±8.3 | * | 1.8±0.8 | 9.6±9.8 | * |
| White-bellied Parrot | 3.4% | 50.5% | 0.8±6 | 36.8±69 | * | 2.9±1.5 | 4.1±2.8 |  | 2.9±1.6 | 5.2±5.5 |  |
| White-eyed Parakeet | 36.3% | 43.8% | 14.3±47 | 513.0±1490 | * | 2.6±1.8 | 6.6±4.9 | * | 4.5±5.0 | 48.8±72.5 | * |
| Yellow-crowned Parrot | 77.8% | 70.7% | 70.7±95 | 72.8±101 | 0.38 | 3.7±2.4 | 3.7±2.1 | 0.47 | 6.7±6.7 | 9.3±8.4 | * |

# Chapter 4: Parrot abundance: detectability and variability with claylick proximity, season and habitat type

## 4.1 SUMMARY

The Amazon basin holds very high parrot richness but almost nothing is known of parrot population densities in the region or how these vary across species, habitats, sites and seasons. Such data are becoming increasingly important as environmental change impacts on increasing areas of the region. Parrots are notoriously difficult to survey, especially in tall and structurally complex forests. A three year survey using a line transect distance sampling method was conducted in floodplain and *tierra-firme* forests at three sites in the Tambopata region of southeast Peru. Observers who contributed less than 100km of transect, even after two months of training, were not as adept at encountering perched parrots and results were discarded. In order to correct for the likely violation of the assumption that all birds on the transect line are detected ($g(0) = 1$) a multiplier based on calling rates of birds was calculated. Multipliers for $g(0)$ differ between species, but not season or diurnal period. This method yielded density estimates 8 - 31 percent higher than those from the standard DISTANCE method. The highest density estimates were ~20 birds per $km^2$, but density estimates for most species were in the order of 0.1-10 per $km^2$. Parrot densities were higher in floodplain forest than in *tierra-firme* forest and densities were significantly lower during the wet season in floodplain forests. The parrot communities of *tierra-firme* forests were similar across sites and seasons, but those in floodplain forests differed widely across sites and seasons. The multipliers produced in this study were produced from a multi-year study. However, the small seasonal variation in call rates suggests that similar multipliers could be produced fairly quickly in conjunction with site-specific surveys in other tropical forests. Doing so will improve density estimates.

## 4.2 INTRODUCTION

Parrots are among the most difficult families of bird in the Neotropics to identify and census (Whitney, 1996, Snyder et al., 2000). Although the presence or absence of parrots is now fairly well documented for the lowland forests of Peru (e.g. Valqui, 2004), few density estimates have been produced (Lloyd, 2004). For some species, such as the Amazonian parrotlet *Nannopsittaca dachillea*, listed as ‘Near Threatened’ (BirdLife International, 2007a), almost no field data are available, while basic density data on even one of the most widespread Amazonian species, the Scarlet macaw *Ara macao*, listed as ‘Least Concern’ (BirdLife International, 2007b) are extremely limited (Karubian et al., 2005). For the long-term management of relatively rare or threatened species, unbiased estimates of density, which incorporate some estimate of detectability, are more valuable than presence/absence or relative abundance, as they can provide managers with comparable survey results over time or space (Buckland et al., 2001).

Recent efforts have been made to estimate macaw populations using Distance sampling techniques (e.g. Haugaasen and Peres, 2008). Distance sampling is the most widely used technique for estimating abundance of wild animal populations (Buckland and Anderson, 2004). Distance sampling methods have now been used in a wide range of habitats and regions, and at a broad range of spatial scales (Buckland et al., 2008). These results are generally favourably reviewed in empirical tests, as long as the important assumptions are addressed (e.g. Hounsome et al., 2005, Nelson and Fancy, 1999). The most critical of the assumptions for standard Distance sampling (apart from accurate species identification) is that subjects on or near the transect line or observation point have to be detected with certainty (assumption of $g(0) = 1$). This assumption is rarely tested, but needs consideration (Bächler and Liechti, 2007) especially in structurally tall and complex tropical forest environments where parrots may spend large amounts of time perched quietly and not vocalizing. Since over 90% of group detections in previous studies have been by call (Lee, 2005), vocalization rate needs to be maintained above a certain level in order to assume that groups will be detected. Violations of distance-sampling assumptions may be frequent in heavily forested habitats, where both availability for detection and probability of detection on the transect line (or point) are likely to be <1 (Gale et al., 2009). I know of no parrot study that has tested this assumption for canopy birds.

Distance sampling and density estimates have been used to determine habitat preferences (Lloyd, 2008), as local patterns of species richness, abundance and composition often vary in response to spatiotemporal fluctuations in resource availability (Bissonette and Storch, 2007). Studies have shown parrot preference for different habitat types or successional zones (Robinson and Terborgh, 1997, Haugaasen and Peres, 2008). The two major forest types in Amazonia are floodplain (inundated) forests and upland *tierra-firme* forests that can be readily determined from satellite images and plant composition on the ground (Salovaaraa et al., 2005). Floodplain forests of western Amazonia tend to be eutrophic (Tuomisto, 2007), and eutrophic forests appear to be more productive and to sustain a greater vertebrate biomass than oligotrophic forests (Peres, 2000). Although seasonal movements have been demonstrated to occur between these forest types in understory birds (Beja et al., 2010), these differences have not been quantified for the canopy specialists such as parrots.

Southeastern Peru has the highest concentration of parrot geophagy sites (claylicks) in the Amazon (Chapter 2). The impact of claylick presence on parrot movements and abundance has not been quantified in any previous study, although Brightsmith (2006) noted a correlation between food abundance, parrot encounter rate, parrot nesting and claylick use at the region’s largest claylick. No study has attempted to quantify the presence of claylick to determine if seasonal changes in encounter rate are dependent or independent of their presence.

### 4.2.1 Aims

Firstly, estimate parrot densities and factors influencing them in lowland Amazon rainforest of southeastern Peru; secondly, check the distance sampling assumption $g(0) = 1$ using a multiplier based on vocalization rates. To achieve this I have the following objectives:

1. Quantify patterns of detection that may influence the assumption $g(0) = 1$
2. Estimate parrot abundance in two major lowland Amazon habitat types (floodplain and *tierra-firme*).
3. Determine seasonal changes in abundance at the landscape level in relation to claylick proximity

## 4.3 METHODS

### 4.3.1 Study site

Bird surveys were conducted at sites within the Tambopata National Reserve (TNR) and associated buffer zone (BZ), southeastern Peru (274,690 ha and 186,450 ha respectively (Salmón et al., 2003)). The reserve lies adjacent to the 1.09 million ha Bahuaja-Sonene National Park. Major forest types according to Salmón (2003) are floodplain (TNR: 32.68%, BZ: 15.44%) and *tierra-firme* (TNR: 62.58%, BZ: 83.17). All sites were located on the Tambopata River, a low-gradient white-water river that meanders through a 5-10 km-wide floodplain and is flanked by terraces up to 30 m high. Surveys were conducted between 350 and 195 m asl. Vegetation is mostly humid subtropical forest. Rainfall ranges between 1600 and 3300 mm and temperature between 10ºC and 38ºC (Räsänen, 1993, Tobler, 2008, Brightsmith, 2004). Research was carried out from three bases: Posada Amazonas lodge (Posada), Refugio Amazonas lodge (Refugio) and Tambopata Research Centre (TRC), all administered by the ecotourism company Rainforest Expeditions. Posada (12° 48.102'S, 69° 18.022'W) is located on the edge of a 2000 ha local community reserve and the Tambopata National Reserve. All transects at this site were within five kilometres of two riverside parrot claylicks. Refugio (12° 52.442'S, 69° 24.641'W) is located 14 km south-west of Posada on a private reserve. The closest parrot claylick is the El Gato claylick complex, over five kilometres west and all sampling was conducted between five and ten kilometres from this claylick. A mammal claylick at Refugio was known to attract *Pyrrhura rupicola*. The region’s largest claylick at TRC (13° 8.088'S, 69° 36.618'W) is 35 km south-west from Refugio and 50 km from Posada.

### 4.3.2 Transect survey

At TRC and Posada five transects were orientated away from the claylick in order to determine the change in encounter rate in relation to distance from the claylick. At Refugio transects were placed in the two major forest types with no specific orientation. Floodplain transects were located mostly in mature forest types, being the representative of the region. *Tierra-firme* forest included no-longer flooded terraces of the Holocene floodplain of the local rivers and ancient Pleistocene alluvial terraces (Räsänen, 1993).

Variable-width line transect surveys were used to estimate the densities of the focal species following the methods of Bibby et al. (1998). Twice per month, between December 2005 and December 2008, up to 15 transects totalling 49 km in length were surveyed, subject to weather and logistical constraints. Morning surveys were conducted from daybreak, which varied from 05h00 in December to 05h45 in July, finishing at 11h00 at the latest. Afternoon surveys were conducted from 15h15 to 17h30. Generating precise density estimates usually requires considerable survey effort to obtain sufficient sample sizes (see Buckland et al., 1993, Buckland et al., 2001). Revisiting survey sites, rather than setting up new ones, has obvious advantages as a means of increasing sample sizes and is used commonly in distance sampling (Buckland et al., 2001, Rosenstock et al., 2002). In order to monitor each kilometre section at the same time of day and the same number of times, during 2006 transects were subdivided into three transects of lengths two, three, four and five kilometres. Sampling was conducted in both directions along the transects. From 2007 to 2008 four kilometre transects along the same routes were conducted to monitor year on year seasonal change in a way that optimised bird detection rate and transect length as transects of greater length showed a marked decrease in group encounter rates four hours after the survey start (Lee, 2006), as observed in other studies from tropical forests (Manu and Cresswell, 2007).

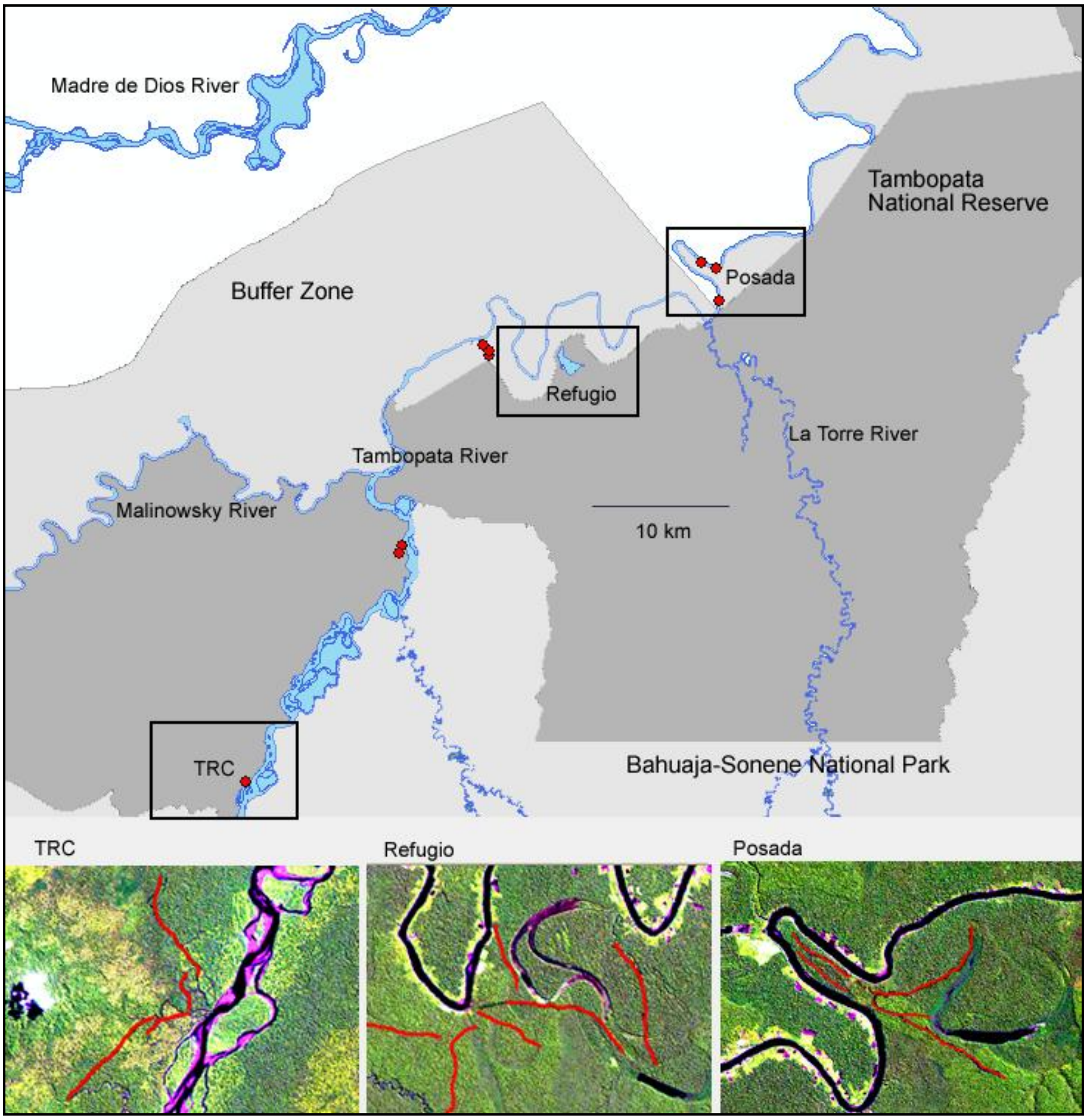

Figure 4.1: The location of the study site showing the protected areas in the main in-set, with parrot claylick locations marked as red points. Satellite images of the three locations show positions of 15 transects in red. Rivers are shown in blue. *Tierra-firme* forest is lighter green while floodplain forest is darker. White patches along the river for *Refugio* and *Posada* indicate small scale agricultural plots. For TRC light green forest associated with the braided river system is successional forest, and yellow forest is associated with large stands of bamboo.

Surveys were carried out throughout the year at Refugio and Posada sites by three main observers (AL and two full-time field assistants – see chapter acknowledgements). Supplementary observation was taken by part-time field assistants. Observers were trained in species identification and visual and aural distance estimation by testing them and then confirming the distance to observed birds and other random objects with a tape measure or rangefinder. The onsite minimum training period (excluding pre-arrival training using online material) was six weeks, with most observers only conducting surveys alone after eight weeks. Observers were rotated among sites to reduce potential observer bias. Group encounter rates and individuals recorded within 30m of the line transect were log transformed and compared with one-way ANOVA and Tukey post-hoc tests to compare among observers. Thirty metres was used as a cut off point as distances beyond this point were more often estimated than measured ($\chi^2_1 = 15.6$, $p < 0.001$) and it is recommended that recorders concentrate on bird detections within 30 m of the line transect (Buckland et al., 2008). Information on group and individual encounter rates are presented as mean ± standard deviation, while density estimates (D) are represented as individuals per square kilometre ± standard error.

On each transect, observers recorded (1) focal species (2) number of individuals and the confidence of the observer of the group count (accurate being more than 90% confident), (3) detection cue (visual, vocal, foraging or wingbeat), (4) activity (perched, flying, perched then flying or flying and then perched, (5) if the encounter was visual or aural only (6) position along the transect, (7) perpendicular distance from the transect line to groups of perched birds up to 200m on either side and 100m ahead or behind of the observer. For aural contacts, mean group size for that species was substituted for the missing group size values. Mean group size was calculated from accurate group counts from towers (see below) for three month intervals, with the appropriate mean for each three month period substituted for missing values. This was done to account for possible changes in group size with season.

### 4.3.3 The influence of call rate on detection probability

Variation in the ability of observers to detect birds is strongly linked to bird vocalization and this can vary on an hourly and seasonal basis (Blake, 1992). Vocalization rates (call rate) was used to calculate approximate values for g(0) for each species of parrot. To attain g(0) = 1, I assumed that an appropriate call rate is a minimum of one vocalization per six minutes, since it takes six minutes to cover 100 meters of transect, with 100m being the length of transect around the observer within which perched groups of birds were recorded.

Call rates of visible birds were monitored from vantage points, which consisted of two 30m+ towers and two 20m+ river bank view-points. Observations were conducted on all groups of flying and perched birds from December 2005 to December 2006, and then only for perched birds until December 2007. The following information was recorded for each encounter: Time of onset of encounter, species, group size, distance from observation point in three distance bands (<100m, 101-200m, >200m) based on key features measured with a rangefinder, number of vocalizations (classified as a discreet note or joined notes of up to 3 seconds in length), and time for the end of the encounter (defined as birds lost from view, change in group size or change in behaviour from perched to flying). Kruskal-Wallis tests were used to test differences in call rate between species and months. Spearman's rank correlations were used to determine relations between body size and call rate.

### 4.3.4 Density calculations

Density estimates were produced using the DISTANCE 5.0 program (Thomas et al., 2006). For software settings, I followed the recommendations of Buckland et al. (2001) and those used by others for estimating the densities of large birds from similar rainforest environments (Kinnaird et al., 1996, Marsden, 1999, Anggraini et al., 2000). For all species, birds were entered as clusters and distance data were grouped into automatic distance bands by the software. Both aural and visual detections were combined. Flying then perched groups were not included in calculating distances as they violate the assumption of distance sampling that only birds originally in the area are recorded (Marsden, 1999). Perched and perched then flying groups are hereon referred to as perched birds except where the difference is important. Models were fitted using the automated sequential selection and the Akaike's Information Criteria (AIC) stopping rule. A sequential testing of the key functions and series expansions were examined to fit detection functions to the data. Key functions (uniform, half-normal and hazard key) with the cosine, simple polynomial and hermit polynomial adjustment terms were tested, as suggested by Buckland et al. (2001).

A variety of truncation distances were tested and it was generally found that truncating the greatest 5-10% of distances for observations usually gave the best model fits, but for species with low encounter rates (<30) or best described by the uniform model truncation was based on the largest observed distance. Truncation distances were chosen based on those that provided the lowest coefficient of variation of the density estimate and then using the lowest AIC function when selecting the best model among those with the same truncation distances and other input parameters, following Buckland et al. (2001). Significant differences between groups were determined using Z-tests.

## 4.4 RESULTS

### 4.4.1 Sample effort and issues with multiple observers

Of the 15 fieldworkers who conducted surveys at Refugio and Posada, there was a marked difference in mean encounter rate between the group who had conducted more than 100 km of transect compared to those who had conducted <100 km (mean >100km: 5.7 ± 8.5; mean <100km: 3.0 ± 4.5; 2-sample t-test, unequal variance: t = 4.13, df = 203, $p < 0.001$). The group of observers who conducted fewer than 100 km and observers from the second group whose detection functions showed severe heaping were discarded for density analysis. In the remaining group of six observers (Table 4.1) the first 100 km of one observer was discarded as detection rates were significantly lower than subsequent observations. One of these observers had a significantly lower individual encounter rate compared to the remaining observers (F = 6.07, df = 5, $p < 0.001$). Comparing with and without this observer using all records there was no significant difference between resulting total parrot density estimates (without: D = 50.5 ± 5.5; with: D = 48.4 ± 4.8; Z = 0.29, $p = 0.61$). This observer’s results were thus incorporated in order to improve coefficients of variation after stratification (stratification being a Distance sampling method for handling heterogeneity in the survey data, of improving precision and reducing bias (Buckland et al., 2001)). The majority of sampling was conducted at two sites (Refugio and Posada), so site results for species density estimates at TRC are indicative only (Table 4.1).

Table 4.1: A summary of observer effort (kilometres) and encounter rate (individuals per kilometre) for six observers who conducted more than 100 km of transects from December 2005 to December 2008.

| | Sample effort (kilometres) | | | | Encounter rate |
|---|---|---|---|---|---|
| | Site: | | | | |
| Observer | Posada | Refugio | TRC | Total | Mean |
| 1 | 403 | 160 | 53 | 616 | 3.7 ± 3.6 |
| 2 | 473 | 522 | 6 | 1001 | 2.8 ± 4.6 |
| 3 | 133 | 251 | | 383 | 1.8 ± 2.8 |
| 4 | 110 | 34 | | 144 | 4.1 ± 8.4 |
| 5 | 72 | 94 | 2 | 168 | 4.1 ± 3.4 |
| 6 | 44 | 56 | | 100 | 4.1 ± 5.2 |
| Total | 1102 | 866 | 61 | 2413 | |

### 4.4.2 Vocalization patterns by species and season

From December 2005 to December 2007, 626 observation sessions (2198 hours) of vocalizing birds were conducted. There was a significant difference between call rate for perched and flying birds (median call rate (calls per minute) perched: 0.9, 0 - 4.3, n = 2542; flying: 15.4, 6.6 - 20, n = 6597; U = 3293329, Z = -45.18, $p < 0.001$). There was no significant difference in call rate for perched birds between morning and afternoon (Posada: U = 250251, Z = -0.75, $p = 0.45$; Refugio: U = 5281.5, Z = -1.44, $p = 0.15$), years (Posada: U = 575942.5, Z = -0.78, $p = 0.44$; Refugio: U = 5281.5, Z = -1.44, $p = 0.15$) or sites (U = 255594, Z = -0.29, $p = 0.77$).

There was a significant difference between call rates among species (Kruskal-Wallis: $\chi^2_{14} = 293.8$, $p < 0.001$). Cobalt-winged Parakeet *Brotogeris cyanoptera* and Blue-headed Parrot *P. menstruus* had higher call rates in June (Kruskal-Wallis: $\chi^2_{11} = 23.7$, $p = 0.014$ and $\chi^2_{11} = 34.6$, $p < 0.001$ respectively). There was a negative correlation between bird size and call rate for birds perched within 100m of the observation point ($r_s = -0.58$, $p = 0.039$, n = 13). There was a negative correlation between length of perch time and vocalization rate ($r_s = -0.02$, $p < 0.001$, n = 2331). There was a significant difference in call rate between groups of birds perched less than a minute compared to those perched longer than one minute (<1 minute: 3.2, 0 - 10.6, n = 364; >1 minute: 0.9, 0 – 3.5, n = 2147; U = 261813, Z = -5.91, $p < 0.001$). Although this may have implications for detectability over the course of the morning if birds rest more and so call less, I did not find a significant decrease in detectability over the monitoring period between hours when monitoring was conducted ($\chi^2_5 = 1.48$, $p$ = 0.915), suggesting that the sampling period was adequate for the purposes of uniform detection.

As calls per six minute period were in some cases extrapolated from events where perched birds where perched for fewer than six minutes, this introduces the danger of overestimating a likelihood of a bird remaining undetectable for the six minute period (a bird that was observed silent for three minutes and then flew off may have called if given the opportunity to remain perched for six minutes). In effect though birds perched less than 6 minutes called significantly more per minute than birds that remained perched for longer than 6 minutes (median <6 minutes: 12, median >6 minutes: 0.6; Mann-Whitney U: $p < 0.001$, n = 9522) since these encounters were due to birds flying off, when vocalisations were higher. For birds that were perched and lost from view, there was no difference between birds recorded for more or less than 6 minutes (median >6 minutes: 0.28, median <6: 0.56; Mann-Whitney U, $p = 0.3$, n = 212), suggesting that upward extrapolation of detection functions based on groups perched for less than six minutes is acceptable. However, detection functions should ideally be based on groups of birds that perched longer than 6 minutes.

### 4.4.3 Estimating values of g(0)

If the basic Distance sampling assumption g(0) = 1 is correct, then the ratio of vocalizing groups to silent groups observed from vantage points should be roughly equivalent to the ratio of groups recorded to vocalize along the transect to groups where no vocalizations were recorded. However, detection rate of silent groups along transects was only 4% (n = 2681) of the total number of groups perched within 30m (a distance most critical for determining detection functions) of the transect for the entire study period, while the proportion of perched groups recorded as silent from vantage points was 29% (n = 971). It is most likely that birds that did not vocalize were not detected and so g(0) = 1 is an invalid assumption.

There was an apparent observer impact on bird behaviour. During transects, perched birds were recorded in three categories: flying then perched, perched then flying and perched only. Theoretically (without bird reaction to recorder presence), one would expect the proportion of flying then perched birds (FP) to equal the perched and then flying birds (PF). However, the PF group were recorded nearly twice as much for encounters within 30m of the transect line (FP = 653, PF = 1110). Since the proportion of events recorded as FP did not differ among observers ($\chi^2_4 = 4.31$, *p* = 0.37) and the distance was significantly less for PF groups compared to FP groups for all detections (median, interquartiles FP = 32 m, 15 – 60 m, n = 651, PF = 27 m, 14 – 50 m, n = 1105; U = 326079, Z = -3.3, *p* = 0.001), an observer presence affect is a likely explanation.

Groups of birds that were perched and then flew called significantly more than perched birds that disappeared in the vegetation or similarly lost from view (median vocalizations for groups that perched then flew: 1.6, 0.5 – 6.2, n = 468; perched and were lost from view: 0.6, 0 – 2.1, n = 175; U = 40682, Z = -6.1, p <0.001), so correction for P and PF groups needs to be treated separately. Thus, a vocalization co-efficient (V) was calculated as follows:

$$V = N - D/N$$

Where N is the total number of observed perched groups of birds from tower surveys, D is the number of groups that vocalized less than once per six minutes. A general multiplier for g(0) was calculated as follows:

$$\text{Multiplier for } g(0) = (\%\text{ encs P} * V_P) + (\%\text{ encs PF} * V_{PF})$$

Where % encs P is the proportion of encounters along transect where perched birds were recorded as perched only; % encs PF is the proportion of encounters along transect where perched birds were recorded as perched and then flying; and $V_P$ and $V_{PF}$ are the vocalization coefficients for the P and PF groups respectively. These values for each species are presented in Table 4.2.

Table 4.2: Multipliers for g(0) for the parrot species of the Tambopata, based on call rate. D = number of groups observed from the tower that vocalized less than once per six minutes; N = total number of groups observed from the tower; V is a vocalization coefficient (N-D/N); % encs = proportion of encounters of either P or PF groups based on total encounters. Multiplier g(0) = (% encs P * $V_P$) + (% encs PF * $V_{PF}$).

| | P | | | | PF | | | | Multiplier |
|---|---|---|---|---|---|---|---|---|---|
| | D | N | V | % encs | D | N | V | % encs | g(0) |
| Black-capped Parakeet | 38 | 151 | 0.75 | 0.47 | 1 | 159 | 0.99 | 0.53 | 0.88 |
| Blue-headed Macaw[+] | 5 | 12 | 0.58 | 0.50 | 5 | 95 | 0.95 | 0.50 | 0.77 |
| Blue-headed Parrot | 229 | 395 | 0.42 | 0.57 | 114 | 746 | 0.85 | 0.43 | 0.60 |
| Blue-and-yellow Macaw | 9 | 26 | 0.65 | 0.58 | 3 | 63 | 0.95 | 0.42 | 0.78 |
| Chestnut-fronted Macaw | 38 | 139 | 0.73 | 0.53 | 24 | 584 | 0.96 | 0.47 | 0.84 |
| Cobalt-winged Parakeet | 29 | 177 | 0.84 | 0.75 | 19 | 1318 | 0.99 | 0.25 | 0.88 |
| Dusky-headed Parakeet | 4 | 17 | 0.76 | 0.54 | 1 | 273 | 1.00 | 0.46 | 0.87 |
| Mealy Parrot | 102 | 316 | 0.68 | 0.77 | 264 | 1526 | 0.83 | 0.23 | 0.71 |
| Orange-cheeked Parrot | 10 | 19 | 0.47 | 0.46 | 0 | 80 | 1.00 | 0.54 | 0.75 |
| Red-bellied Macaw[+] | 2 | 5 | 0.6 | 0.73 | 7 | 62 | 0.89 | 0.27 | 0.68 |
| Red-and-Green Macaw | 148 | 637 | 0.77 | 0.73 | 102 | 960 | 0.89 | 0.27 | 0.80 |
| Scarlet Macw | 83 | 296 | 0.72 | 0.67 | 32 | 259 | 0.88 | 0.33 | 0.77 |
| White-bellied Parrot | 38 | 305 | 0.88 | 0.64 | 9 | 124 | 0.93 | 0.36 | 0.90 |
| White-eyed Parakeet | 3 | 5 | 0.4 | 0.38 | 0 | 77 | 1.00 | 0.62 | 0.88 |
| Yellow-crowned Parrot | 13 | 41 | 0.68 | 0.86 | 50 | 271 | 0.82 | 0.14 | 0.70 |
| *Aratinga** | | | | | | | | | 0.88 |

*A modified multiplier was calculated for the *Aratinga* species as too few perched events were recorded at the species level (White-eyed Parakeet *A. leucophthalma* (5) and Dusky-headed Parakeet *A. weddellii* (17))

[+] Results for Blue-headed Macaw *P. couloni* and Red-bellied Macaw *O. manilata* are provided for information only, as densities are based on stratification of results from Chestnut-fronted Macaw *A. severus*

Calculation of density estimates using the multiplier used a different subset of data based on detection cue compared to standard distance sampling. Standard density estimations used all distances for perched birds regardless of method of detection, while corrected values were based on distances for perched birds where the cue was auditory, as the multiplier was valid for auditory cues only. Corrected values were used for forest type, site and season stratifications.

### 4.4.4 Density estimates by site, season and habitat

Sufficient encounters (>30) were obtained to calculate density estimates for 15 of 18 parrot species encountered on transects, either directly or via stratification using detection function of related species for species with low detection rates. Regional density estimates for Blue-headed Macaw *Primolius couloni* and Dusky-headed Parakeet *Aratinga weddelli* were based on detection functions for Chestnut-fronted Macaw *Ara severus* and White-eyed Parakeet *Aratinga leucophthalma* respectively, as they are roughly equivalent sizes and occupy similar habitats (Juniper and Parr, 1998). Resulting density estimates should be treated with caution (see Manu and Cresswell, 2007). Although Red-bellied Macaw *Orthopsittaca manilata* is similar in size to *Ara severus*, habitat use and flock size differences suggested against calculating density estimates for this species based on stratification, so results should be considered comparative only. Insufficient encounters were obtained for the three parrotlet species (Dusky-billed Parrotlet *Forpus modestus*, Amazonian Parrotlet *Nannopsittaca dachilleae* and Scarlet-shouldered Parrotlet *Touit huetii*) to allow either individual density calculations or to allow density estimation by species stratification (the later two species were never encountered perched along transects). Three species recorded in other parts of the Tambopata region were never recorded by observers: Red-shouldered Macaw *Diopsittaca nobilis,* Rose-fronted Parakeet *Pyrrhura roseifrons* and Tui Parakeet *Brotogeris sanctithomae*.

Density estimates using the multiplier were significantly higher compared to standard distance sampling for two species: Mealy Parrot *Amazona farinosa* and Blue-headed Parrot *Pionus menstruus* (Table 4.3). These were species with the highest number of detections and the greatest multiplier respectively. The species with the highest density was Mealy Parrot *Amazona farinosa* (14.74 ± 1.78 ind/km$^2$), while Blue-headed Macaw *Primolius couloni* had the lowest density (0.06 ± 0.05 ind/km$^2$).

Table 4.3: Density estimates for 14 parrot species within the Tambopata region of southeastern Peru, comparing standard Distance sampling to results obtained using multipliers based on detection function. n = number of detections, D = density (individuals per square kilometre), se = standard error. Significance at the 0.05 level are indicated by * with Z scores.

| | Standard Distance sampling | | Density using multiplier for g(0) | | |
|---|---|---|---|---|---|
| Species | D ± se | N | D ± se | n | Z |
| Black-capped Parakeet | 7.3 ± 1.09 | 335 | 8.09 ± 1.21 | 325 | -0.49 |
| Blue-headed Macaw[++] | 0.06 ± 0.04 | 7 | 0.06 ± 0.05 | 6 | -0.01 |
| Blue-headed Parrot | 1.95 ± 0.29 | 246 | 2.84 ± 0.41 | 228 | -1.78* |
| Blue-and-yellow Macaw | 0.32 ± 0.08 | 59 | 0.37 ± 0.09 | 55 | -0.39 |
| Chestnut-fronted Macaw[++] | 0.27 ± 0.19 | 24 | 0.18 ± 0.09 | 19 | 0.42 |
| Cobalt-winged Parakeet | 10.36 ± 2.11 | 394 | 11.59 ± 2.33 | 377 | -0.39 |
| Dusky-headed Parakeet[+] | 0.94 ± 0.59 | 27 | 0.66 ± 0.41 | 26 | 0.38 |
| Mealy Parrot | 10.89 ± 1.31 | 1617 | 14.74 ± 1.78 | 1551 | -1.74* |
| Orange-cheeked Parrot | 0.72 ± 0.16 | 75 | 1 ± 0.21 | 69 | -1.04 |
| Red-and-Green Macaw | 1.78 ± 0.31 | 374 | 2.17 ± 0.38 | 358 | -0.78 |
| Scarlet Macaw | 1.47 ± 0.49 | 233 | 1.74 ± 0.62 | 219 | -0.33 |
| White-bellied Parrot | 10.16 ± 0.61 | 659 | 11.03 ± 0.69 | 635 | -0.94 |
| Red-bellied Macaw | 0.61 ± 0.33 | 12 | 0.61 ± 0.37 | 11 | 0.00 |
| White-eyed Parakeet[+] | 0.75 ± 0.28 | 47 | 0.96 ± 0.39 | 45 | -0.44 |
| Yellow-crowned Parrot | 0.72 ± 0.17 | 112 | 1.03 ± 0.24 | 112 | -1.04 |

[+] *Aratinga* density based on common detection function, stratified by species

[++] *P. couloni* and *A. severus* density based on common detection function, stratified by species. *O. manilata* density based on *A. severus* detection function.

On transects that radiated away from a claylick, there was a significant difference in mean encounter rates among sections of one kilometre length of transect for 14 of 18 parrot species (1-way ANOVA, see Appendix 4.1). Overall, perched parrot encounter rate decreases with distance from claylick (Figure 4.2). Species where Tukey-post hoc tests indicated the first or first and second kilometres formed homogenous subsets included: Blue-headed Macaw *P. couloni*, Blue-headed Parrot *P. menstruus*, Chestnut-fronted Macaw *A. severus*, Cobalt-winged Parakeet *B. cyanoptera*, Mealy Parrot *A. farinosa*, Scarlet Macaw *A. macao*, Red-and-Green Macaw *A. chloropterus*, White-eyed Parakeet *A. leucophthalma* and Yellow-crowned Parrot *A. ochrocephala*. These are all species observed at claylicks at both Posada and TRC. White-bellied Parrot *Pionites leucogaster*, recorded on the claylick only at TRC, was encountered more on the further sections of the transects. In order to account for claylick presence in density estimates, 280 km of transect conducted in the morning within two kilometres of the claylick at Posada were excluded to provide an alternate measure of density for this site (Table 4.4).

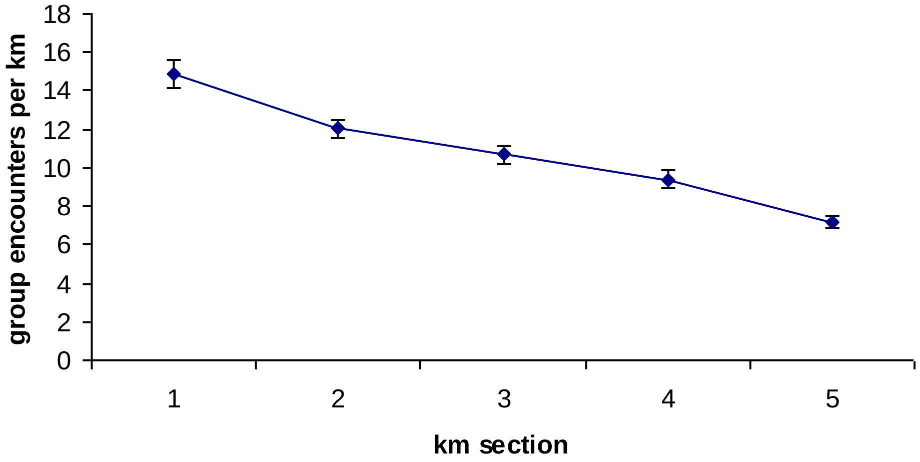

Figure 4.2: Change in parrot group encounter rate with distance (kms) from claylicks for five transects orientated away from claylicks. Bars for mean line represent standard error.

Overall, there was no significant different in parrot density between Posada and Refugio (Posada: D = 58.9 ± 9.67, Refugio: D = 49.3 ± 7.97, Z = 0.77, $p > 0.05$). Of the two species more abundant at Refugio than Posada (Table 4.4), Scarlet Macaw *Ara macao* uses the claylick at Posada rarely, while Blue-and-Yellow Macaw *Ara ararauna* never uses the claylick. Four species were more abundant at Posada than Refugio (Table 4.4): Black-capped Parakeet *P. rupicola*, Blue-headed Parrot *P. menstruus*, Yellow-crowned Parrot *A. ochrocephala* and Red-and-green Macaw *A. chloropterus.* All these species frequently use the claylick at Posada.

Table 4.4: Density estimates for 11 parrot species at three sites in the Tambopata region. Density estimates at sites are provided for all transects and for transects conducted beyond 2km from a claylick (>2km). Z values are shown for differences between Posada and Refugio, with $p < 0.05$ indicated by *. TRC results are presented for comparison only due to low sample size.

| | | Posada | Refugio | | TRC |
|---|---|---|---|---|---|
| | | D ± se | D ± se | Z | D ± se |
| Black-capped Parakeet | Overall | 10.66 ± 2.18 | 5.76 ± 1.42 | 1.88* | 0 |
| | >2km | 9.42 ± 2.19 | 5.65 ± 1.43 | 1.44 | 0 |
| Blue-headed Parrot | Overall | 4 ± 0.67 | 1.73 ± 0.45 | 2.80* | 7.34 ± 6.19 |
| | >2km | 3.44 ± 0.95 | 1.68 ± 0.42 | 1.70* | |
| Blue-and-Yellow Macaw | Overall | 0.21 ± 0.06 | 0.49 ± 0.1 | -2.33* | 3.59 ± 4.06 |
| | >2km | 0.2 ± 0.07 | 0.48 ± 0.1 | -2.26* | |
| Cobalt-winged Parakeet | Overall | 14.27 ± 2.94 | 9.18 ± 4.27 | 0.98 | 1.83 ± 1.47 |
| | >2km | 13.09 ± 3.02 | 9.43 ± 4.3 | 0.7 | |
| Mealy Parrot | Overall | 16.98 ± 3.65 | 12.12 ± 2.39 | 1.12 | 17.33 ± 3.52 |
| | >2km | 11.35 ± 2.46 | 11.24 ± 2.19 | 0.03 | |
| Orange-cheeked Parrot | Overall | 0.9 ± 0.17 | 0.96 ± 0.33 | -0.16 | 3.97 ± 3.33 |
| | >2km | 0.94 ± 0.2 | 1.08 ± 0.38 | -0.32 | |
| Red-and-green Macaw | Overall | 3.04 ± 0.75 | 1.15 ± 0.16 | 2.47* | 3.56 ± 0.6 |
| | >2km | 2.82 ± 0.69 | 1.15 ± 0.15 | 2.36* | |
| Scarlet Macaw | Overall | 1.01 ± 0.18 | 1.99 ± 0.27 | -3.04* | 12.25 ± 4.93 |
| | >2km | 1.07 ± 0.22 | 1.96 ± 0.27 | -2.59* | |
| White-bellied Parrot | Overall | 11.78 ± 1.03 | 10.62 ± 0.95 | 0.83 | 3.61 ± 0.64 |
| | >2km | 11.76 ± 1.09 | 10.54 ± 1.06 | 0.8 | |
| White-eyed Parakeet | Overall | 0.66 ± 0.37 | 1.11 ± 0.71 | -0.56 | 1.53 ± 0.63 |
| | >2km | 0.44 ± 0.45 | 1.11 ± 0.73 | -0.78 | |
| Yellow-crowned Parrot | Overall | 1.45 ± 0.47 | 0.61 ± 0.18 | 1.67* | 0.28 ± 0.14 |
| | >2km | 0.9 ± 0.34 | 0.5 ± 0.15 | 1.05 | |

Blue-headed Parrot *Pionus menstruus* was the only species of 11 to show a regional change in abundance between the dry and wet season (wet: D = 1.9 ± 0.41, dry: D = 3.2 ± 0.64, Z = -1.75, $p < 0.05$), although Orange-cheeked Parrot *Pyrilia barrabandi* shows a seasonal difference in abundance at Posada (wet: 0.6 ± 0.14, dry: 0.3 ± 0.09, Z = 1.89, $p < 0.05$). For the seven species for which stratification at the 3-month level could be reliably performed, all but the two red *Ara* species showed some degree of significant difference among seasons (Figure 4.3).

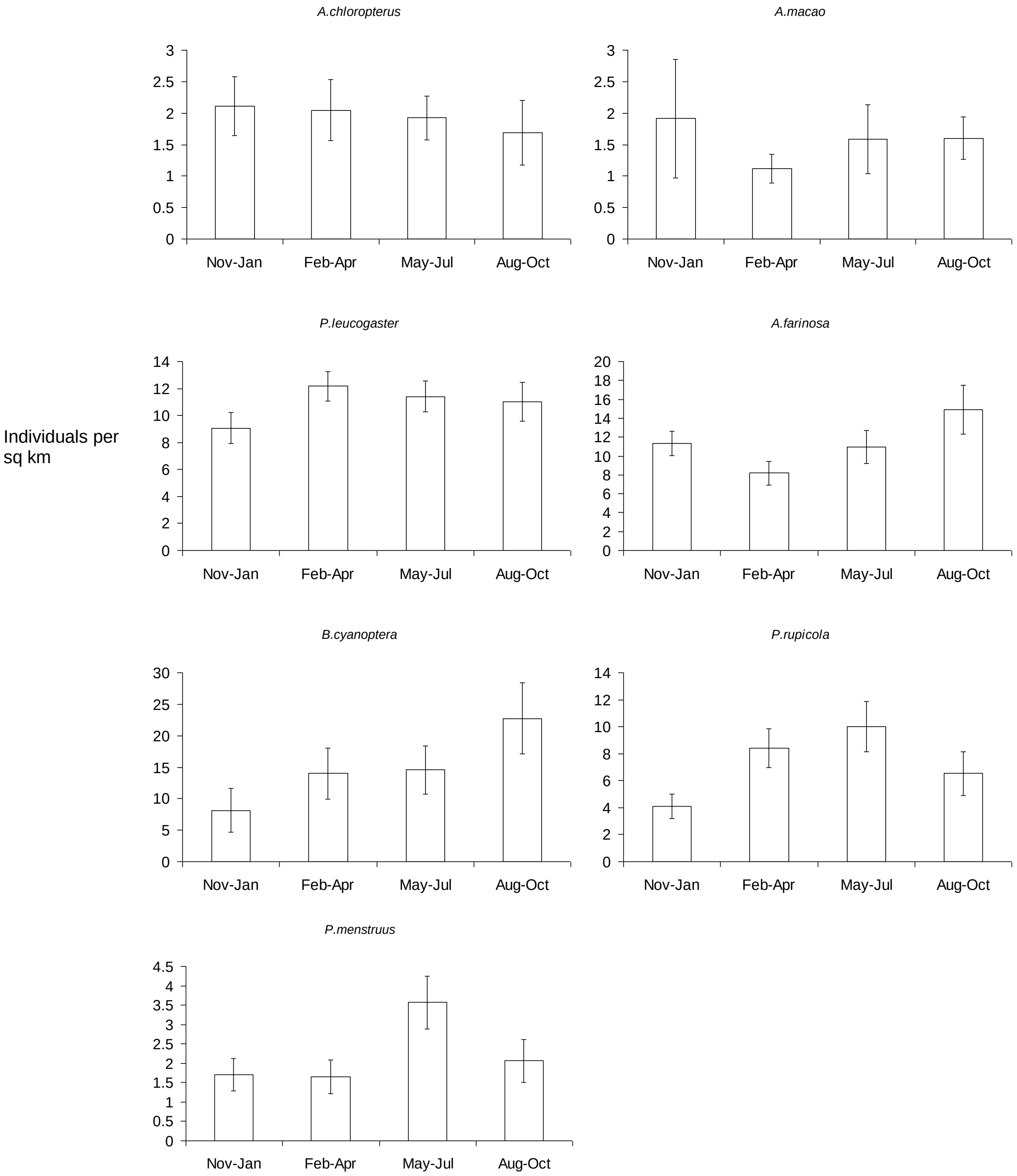

Figure 4.3: Regional density estimates, excluding transects within 2 km of a claylick, for seven parrot species stratified by three month periods. Error bars represent ± 1 standard error.

Overall, parrot density was significantly higher in floodplain forest than *tierra-firme* forest (floodplain: 68.2 ± 5.59, *tierra-firme*: 37.59 ± 4.56; Z = 4.24, $p < 0.05$). Five of eleven species occur at significantly higher densities in floodplain forest, while none are found at higher densities in *tierra-firme* forest (Table 4.5). At the seasonal level, there were significantly more parrots during the dry season than in the wet season (dry: 73.42 ± 6.77; wet: 57.7 ± 4.96; Z = -1.87, $p < 0.05$), but this difference was not seen for *tierra-firme* forest where overall parrot density was higher in the wet season (dry: 32.37 ± 3.37; wet: 36.8 ± 4.76; Z = 0.76, $p > 0.05$). No species show significant seasonal differences in density in *tierra-firme* forest, while four of ten species occur at significantly higher abundance during the dry season in floodplain forest (omitting transects within 2 km of claylicks).

Table 4.5: Parrot density (D) stratified by habitat type for floodplain and *tierra-firme* forest types. Species with significant differences between forest types are indicated by * at the 0.05 level, which a difference in season for a forest type is shown by $^{+}$ within D values.

| | Floodplain | *Tierra-firme* |
|---|---|---|
| | **D** ± se | **D** ± se |
| Black-capped Parakeet | 9.94 ± 1.22 | 4.0 ± 1.12* |
| Wet season | 9.47 ± 1.51 | 3.11 ± 0.69 |
| Dry season | 12.41 ± 1.67 | 3.37 ± 1.24 |
| Blue-headed Parrot | 2.84 ± 0.37 | 2.23 ± 0.96 |
| Wet season | 2.1 ± 0.55 | 1.54 ± 0.6$^{+}$ |
| Dry season | 3.96 ± 0.57 | 2.3 ± 1.22$^{+}$ |
| Blue-and-yellow Macaw | 0.41 ± 0.11 | 0.35 ± 0.15 |
| Wet season | 0.2 ± 0.09 | 0.37 ± 0.21$^{+}$ |
| Dry season | 0.56 ± 0.16 | 0.22 ± 0.08$^{+}$ |
| Cobalt-winged Parakeet | 16.52 ± 3.19 | 4.33 ± 1.45* |
| Wet season | 11.42 ± 3.11 | 4.4 ± 1.77$^{+}$ |
| Dry season | 20.67 ± 3.65 | 4.48 ± 1.66$^{+}$ |
| Mealy Parrot | 14.93 ± 1.66 | 7.45 ± 0.75* |
| Wet season | 14.3 ± 1.37 | 8.06 ± 0.93 |
| Dry season | 16.29 ± 2.3 | 6.98 ± 1.27 |
| Orange-cheeked Parrot | 0.88 ± 0.19 | 1.45 ± 0.5 |
| Wet season | 1.72 ± 0.85 | 1.81 ± 0.88 |
| Dry season | 0.77 ± 0.24 | 0.66 ± 0.3 |
| Red-and-green Macaw | 2.47 ± 0.56 | 1.36 ± 0.28* |
| Wet season | 2.6 ± 0.68 | 1.78 ± 0.49 |
| Dry season | 2.33 ± 0.6 | 1.01 ± 0.17 |
| Scarlet Macaw | 1.68 ± 0.61 | 2.01 ± 1.18 |
| Wet season | 1.8 ± 1.05 | 1.92 ± 1.28 |
| Dry season | 2.46 ± 0.84 | 1.72 ± 0.79 |
| White-belled Parrot | 11.17 ± 0.91 | 10.56 ± 1.26 |
| Wet season | 11.25 ± 0.96 | 10.44 ± 1.63 |
| Dry season | 13.15 ± 1.2 | 9.62 ± 1.37 |
| Yellow-crowned Parrot | 0.98 ± 0.22 | 0.31 ± 0.07* |
| Wet season | 0.48 ± 0.2 | 0.41 ± 0.1$^{+}$ |
| Dry season | 1.34 ± 0.35 | 0.23 ± 0.06$^{+}$ |
| White-eyed Parakeet | 0.97 ± 0.59 | 0.57 ± 0.34 |

## 4.5 DISCUSSION

### 4.5.1 Neotropical parrot density estimates

Very few density estimates have been produced for any parrot population in South America. However, where they do exist our results are comparable to those from other Neotropical bird surveys for the same species or genera (Table 4.6). Density estimates for Scarlet Macaw *A. macao,* Red-and-Green Macaw *A. chloropterus,* Black-capped Parakeet *P. rupicola,* Orange-cheeked Parrot *P. barrabandi* and White-belled Parrot *P. leucogaster* were similar or comparable to those from nearby Manu (Terborgh et al., 1990), although the regional Mealy Parrot *A. farinosa* densities are much higher especially considering the earlier study was conducted in floodplain type forest only. Mealy Parrot *A. farinosa* densities are also slightly higher than those from Guatemala which are 7.4 to 9.2 ind/km$^2$ (Bjork, 2004), but in line with 13.82 ± 5.9 ind/km$^2$ reported from an Atlantic rainforest island reserve (Guix et al., 1999). In a survey of the Sooretama/Linhares reserves in Atlantic forest reserve, Brazil (Marsden et al., 2001) Blue-headed Parrot *Pionus menstruus* density was 2.33, very comparable to the regional 2.87 ind/km$^2$ of this study. Although the Atlantic site had too few Mealy Parrot *A. farinosa* to calculate abundance, the Red-browed Amazon *Amazona rhodocorytha* 13.1 ± 28 is within the expected range for the dominant *Amazona.* Bahama parrot Amazona *leucocephala bahamensis,* for instance, occurs at densities from 15 ± 4.2 to 18 ± 4.9 ind/km$^2$ (Rivera-Milan et al., 2005). Scarlet Macaw *A. macao* and Red-and-green Macaw *A. chloropterus* densities were similar to results from two other western Amazon studies (Lloyd, 2004, Haugaasen and Peres, 2008), but Blue-and-yellow Macaw *A. ararauna* densities were the lowest of any comparable study. The density estimates for Blue-headed Macaw *P. couloni* are within the range predicted by Tobias and Brightsmith (2007) of 0.02 - 0.1 individual / km$^2$.

Table 4.6: A comparative table of density estimates (individuals / $km^2$) from other Meso- or South American studies. FP = Floodplain; TF = *Tierra-firme*; too few = too few encounters to estimate density.

| | Bonadi and Bacon 2000 | Guix 1999 | Hauggeson and Perez 2008 | Lloyd 2004 | Marsden et al 2000[a] | Terborgh et al 1990[b] |
|---|---|---|---|---|---|---|
| *P. rupicola* | | | | | | 7 |
| *P. couloni* | | | | | | too few |
| *P. menstruus* | | | | | 2.3 | too few |
| *A. ararauna* | | | FP: 1.1 ± 0.3,<br>TF: 0.9 ± -0.3 | FP: 1.1 - 3.4 ± 4.9<br>TF: too few | | 2 |
| *A. severus* | | | | | | 2 |
| *B. cyanoptera* | | | | | | 32 |
| *A. weddellii* | | | | | | too few |
| *A. farinosa* | | 13.82 ± 5.94 | | | too few | 4 |
| *P. barrabandi* | | | | | | 1 |
| *A. chloropterus* | | | FP - 8.76 ± 0.9<br>TF - 1.8 ± 0.4 * | FP - 1.3 - 2.0 ± 4.9,<br>TF - 1.3 ± 6.6 | | 2 |
| *A. macao* | | | | FP - 0.5 - 2.6 ± 3.0,<br>TF – 0 | | 2 |
| *P. leucogaster* | | | | | | 12 |
| *O. manilata* | 0.5** | | | | | too few |
| *A. leucophthalma* | | | | | too few | 6 |
| *A. ochrocephala* | | | | | | 2 |
| *Other:* | *Amazona aestiva*: 0.3 | *Brotogeris tirica*: 15.05 ± 4.87, *Pyrrhura frontalis*: 13.06 ± 5.53 | *Ramphastos* spp: TF 12.56 ± 1.04, Varzea 4.41 ± 0.55 | | *Brotogeris tirica*: 28; *Pyrrhura cruentata*: 41 | |

* Red macaws include Scarlet Macaw *A.macao* and Red-and-Green Macaw *A. chloropterus;* results for FP are those provided for várzea forest
** Calculated from individuals (224) / area ($450km^2$)
[a] Results for Sooretama/Linhares reserves
[b] Results for Floodplain forest (and equivalent to Robinson and Terborgh (1997))

I am thus confident that the results represent bird densities for the two major forest types in southeastern Peru. However, the survey design did not adequately account for birds in secondary (successional) habitats or palm swamps. Although these habitats form a minor proportion of the overall Tambopata landscape they are very important seasonally (Cowen, 2008) and for habitat specialists, such as Red-bellied Macaw *O. manilata* (Bonadie and Bacon, 2000).

### 4.5.2 The influence of claylicks, habitat and season on parrot abundance

None of the parrot surveys from western Amazon that have produced density estimates have considered the impact of season, despite studies indicating that seasonal movements do occur at least on a regional level (Renton, 2002, Karubian et al., 2005). Seasonal changes in density related to habitat types appear to be more important than seasonal movements related to claylick presence as most species showed seasonal increases in floodplain forest during the dry season regardless of claylick use (see Chapter 3). Seasonal changes were found only for two species in relation to claylick presence (Blue-headed Parrot *P. menstruus* and Orange-cheeked Parrot *P. barrabandi*). Although peak densities did correspond to peak claylick use for Cobalt-winged Parakeet *B. cyanoptera* (Chapter 3), it is less clear if this species simply uses claylicks more in association with movements to floodplain forest or are an artefact of breeding, which can result in changes in group sizes (Matuzak and Brightsmith, 2007).

Most publications focus on bird abundance or ecology in floodplain forests (Robinson and Terborgh, 1997, Lloyd, 2004), while *tierra-firme* forest is more extensive (80% of Peruvian Amazonia (Salo et al., 1986)) and will come under increased threat as the network of roads grows across the region. Lloyd (2004) encountered no Scarlet Macaw *A. macao* in the *tierra-firme* forest type sampled, while I detected no difference in density between forest types for this species. Known important food plants for *A. macao* are known to occur in *tierra-firme* forest (Trivedi et al., 2004, Haugaasen, 2008).

Although this study did not show a significant difference between dry and wet season in *tierra-firme* forest, overall abundance was higher during the wet season. Since *tierra-firme* represents a considerably larger proportion of the landscape it is possible populations from floodplain forest during the wet season are diluted (the proportional density increase in *tierra-firme* forest would have been lower) and the statistical analysis (sensitive to large variation) may not have been sufficient to detect this seasonal movement. *Mauritia* palm swamps, which account for approximately 5% of the protected area system, may also account for wet season changes in abundance as this palm fruits from September to April (Manzi and Coomes, 2009) and is an important food resource for large macaws and parrots (Brightsmith and Bravo, 2006). Our understanding of local movements and parrot ecology would be greatly enhanced by a study focusing on this forest type.

Encounter rates for species that use claylicks is highest within a kilometre of a claylick. Yellow-crowned Parrot *A.. ochrocephala* and Black-capped Parakeet *P. rupicola* showed clear differences in density estimates between Posada and Refugio that could be accounted for by claylick presence. Blue-headed Parrot *P. menstruus* and Red-and-green Macaw *A. chloropterus* densities may also be influenced by claylick presence. Since bird densities between sites was not significantly different, elevated detection rates around claylicks are most likely due to ‘in transit’ birds, i.e. the area around a claylick is unlikely to support a higher density of birds, which is more likely to be influenced by food and nest site availability. Detection rates between sites outside of claylick high seasons are comparable (Lee, 2009). Bird survey design should consider the presence of geophagy sites for any species that may engage in geophagy and should not be located within two kilometres of a geophagy site.

### 4.5.3 Implications for avian surveys in rainforests

There is concern about observer bias in bird counts that needs to be addressed in every bird survey. We followed recommendations of Buckland et al. (2001) and provided an extensive training period before observers’ records were considered. Even so, the complexity of tropical environments showed that observers who recorded fewer than 100 km of transect even after the training period had a lower detection rate than those who conducted more transects. The impact of observers on ground dwelling birds is of great concern for distance surveys where initial positions need to be recorded accurately (Buckland et al., 2008). I show that canopy dwelling parrots are also influenced by observer presence. As a result, many other species in tropical forest environments may also be influenced by observers. Marsden (1999) recommends an extended count period for parrots and a controlled flush to ensure all birds are counted. It would appear that this flush action occurred naturally during the transect surveys and that this offset the issue of reduced detectability of naturally resting groups of birds. I could not quantify if the flush was entire or partial, and flushing rates could be influenced by time of day, season and degree of human habituation. Correction factors should ideally thus be site and season specific and future studies should attempt to address these issues.

The study is the first non-telemetry study to attempt to address detectability and the first to do so for parrots. In this habitat with a high and dense canopy, the Distance sampling assumption g(0) = 1 cannot be considered valid. Using a multiplier based on detection cue increased densities 8 - 31%. Despite this, for only two species were corrected values significantly higher compared to standard Distance calculations. This low number of species showing a significant difference may in part be explained by the natural flush affect due to the presence of the observer, but may also be due to the large variation displayed in the results. A survey with an increased number of transects in an area with birds habituated to human presence may be more sensitive to the difference between standard distance sampling and sampling based on a multiplier such as the one here based on call rate.

Distance sampling using line transects was inadequate for quantifying abundance for the three species of parrotlet that occur in the region. It is unlikely that point transects would be an adequate alternative for focusing on these species. This methodology when used in Atlantic rainforest also failed to quantify density for the parrotlet species there (Marsden et al., 2000). Although distance sampling has been used to calculate densities for Green-rumped Parrotlet *Forpus passerinus* (Casagrande and Beissinger, 1997), this species occurs in open habitats. Alternate sampling techniques (e.g. spot mapping, look-down surveys or roost counts) may be better for monitoring parrotlet populations in rainforest environments where the small size and soft calls make these small species unsuited for standard Distance sampling surveys. Similarly, the *Mauritia* palm swamp specialists Blue-and-Yellow Macaw *A. ararauna* and Red-bellied Macaw *O. manilata* would be best surveyed using roost counts or spot mapping in their preferred habitats. Red-bellied Macaw *Orthopsittaca manilata* was common on the region’s largest claylick (Brightsmith, 2004) and also commonly observed during a concurrent flight direction study (Ward, 2007) and persists in fragmented or relict habitats where *Mauritia* palms exist (Lees and Peres, 2007). It nests exclusively in *Mauritia* palms (Brightsmith, 2005, Bonadie and Bacon, 2000) and feeds almost exclusively on fruit in this habitat (Bonadie and Bacon, 2000), and is thus rare in the surrounding habitats.

The scale of resolution was course, and allowed analysis on a three month basis for less than half the surveyed assemblage and even so coefficients of variation were generally above the recommended 20% (Marsden, 1999). Future studies would greatly benefit from a larger sample of transects. Since call rate and detection function changes little through seasons, indices (e.g. individuals per kilometre) obtained while working towards Distance sampling also provide useful information when looking for month on month changes, and can easily be correlated with environmental variables such as fruit availability or claylick use.

Determining call rates is relatively straight forward compared to double observer and mark-recapture-distance-sampling techniques (Buckland et al., 2004); can be achieved by single observers; and are relatively straight forward to implement as multipliers in either conventional distance sampling or multiple covariate distance sampling analysis. Although an extensive period was dedicated to collecting information on cue-rate in this study, the results suggest that since cue-rate was not impacted by season, that a relatively short and focused study should allow researchers to obtain correction factors fairly quickly (at least in Neotropical environments and probably humid tropical areas generally). By doing so, surveys producing bird density estimates in rainforest environments can be presented with greater confidence.

### 4.5.4 Conservation implications

This study is the most comprehensive population survey of parrots in southeastern Peru to date. Yet obtaining density estimates for rare species – those of greatest conservation concern – were unsatisfactory. Furthermore, densities fluctuate by season and by habitat. Density figures are fundamental to estimating population sizes to determine the threatened status of any species. How we get a density estimate for conservation purposes remains a big challenge, but one worth pursuing as the current general lack of densities for birds makes estimating global population sizes complicated.

Both claylick presence and, more importantly, forest type clearly have an impact on bird abundance. The floodplain forests of south-east Peru represent the most threatened forest types of the region (Phillips et al., 1994). Floodplain forests are less extensive than upland *tierra-firme* forests, and mature floodplain forests in western Amazonia are being deforested faster than other lowland forest types as human settlement and agriculture spread outward from riverbanks (Phillips et al., 1994). Keystone nesting resources are found predominantly in this habitat type (Brightsmith, 2005). However, seasonal changes in density suggest movements between habitat types which strongly argues for a comprehensive and large-scale habitat management plan. Conservation of claylicks and large areas of associated forest should be of high priority to natural area managers if sustainable economic practices such as ecotourism are to be maintained.

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Appendix 4.1: Mean encounter rate for groups of perched parrots per kilometre section of transect for five transects that radiate from a claylick location. F and p represent results of 1-way ANOVA testing between transect sections.

| Species | 1 | 2 | 3 | 4 | 5 | F | p |
|---|---|---|---|---|---|---|---|
| Amaz. Parrotlet | 0±0 | 0±0 | 0±0 | 0.004±0.004 | 0.004±0.004 | 1.042 | 0.384 |
| Black-cap. Parakeet | 0.394±0.042 | 0.600±0.043 | 0.507±0.048 | 0.367±0.048 | 0.296±0.039 | 7.489 | < 0.001 |
| Blue-head. Macaw | 0.119±0.022 | 0.066±0.013 | 0.072±0.015 | 0.056±0.015 | 0.028±0.012 | 3.934 | 0.003 |
| Blue-head. Parrot | 1.566±0.122 | 1.433±0.102 | 1.200±0.095 | 0.941±0.096 | 0.534±0.060 | 14.768 | < 0.001 |
| Blue/Yellow Macaw | 0.691±0.098 | 0.421±0.051 | 0.466±0.061 | 0.478±0.072 | 0.522±0.065 | 2.362 | 0.051 |
| Chest. Front. Macaw | 1.080±0.096 | 0.609±0.059 | 0.546±0.067 | 0.433±0.073 | 0.233±0.034 | 18.41 | < 0.001 |
| Cob.wing. Parakeet | 1.914±0.161 | 2.334±0.137 | 1.567±0.099 | 1.341±0.091 | 1.036±0.089 | 16.281 | < 0.001 |
| Dusky-bill. Parrotlet | 0.000±0.000 | 0.005±0.003 | 0.003±0.003 | 0.000±0.000 | 0.004±0.004 | 0.646 | 0.63 |
| Dusk-head.Parakeet | 0.596±0.059 | 0.402±0.044 | 0.215±0.029 | 0.256±0.039 | 0.182±0.029 | 15.015 | < 0.001 |
| Mealy Parrot | 4.156±0.308 | 2.685±0.156 | 2.943±0.172 | 2.696±0.165 | 2.063±0.157 | 13.549 | < 0.001 |
| Orange.cheek Parrot | 0.425±0.062 | 0.264±0.029 | 0.301±0.033 | 0.319±0.039 | 0.265±0.040 | 2.601 | 0.035 |
| Red-bell. Macaw | 0.162±0.027 | 0.096±0.016 | 0.149±0.026 | 0.078±0.019 | 0.111±0.026 | 2.4 | 0.048 |
| Red/green Macaw | 1.339±0.096 | 1.313±0.077 | 1.075±0.081 | 0.711±0.070 | 0.530±0.053 | 18.873 | < 0.001 |
| Scarlet Macaw | 1.235±0.125 | 0.687±0.066 | 0.654±0.067 | 0.641±0.068 | 0.403±0.049 | 13.393 | < 0.001 |
| Scarlet should Parrotlet | 0.000±0.000 | 0.000±0.000 | 0.006±0.004 | 0.000±0.000 | 0.000±0.000 | 1.908 | 0.107 |
| White bellied Parrot | 0.370±0.038 | 0.482±0.038 | 0.534±0.043 | 0.693±0.054 | 0.688±0.060 | 8.427 | < 0.001 |
| White-eye. Parakeet | 0.376±0.073 | 0.339±0.044 | 0.304±0.045 | 0.219±0.034 | 0.178±0.030 | 2.507 | 0.04 |
| Yellow.crown. Parrot | 0.419±0.044 | 0.313±0.034 | 0.134±0.023 | 0.170±0.031 | 0.119±0.028 | 14.511 | < 0.001 |
| Total | 14.844±0.735 | 12.049±0.466 | 10.678±0.458 | 9.400±0.459 | 7.194±0.329 | 27.255 | < 0.001 |

# Chapter 5: Habitat selection and dietary metrics in relation to claylick use for a parrot assemblage in southeastern Peru

## 5.1 SUMMARY

Information on parrot diet is under represented in the literature and food resource preferences are a matter of speculation. The role of diet and habitat selection in claylick use are presented here by examining a range of dietary, habitat and abundance variables with two indices of claylick use. Daily claylick use was determined from counts of birds on the claylick; and an index of species level claylick need was estimated as the proportion of the local population visiting the claylick on a daily basis. Parrot density in floodplain and *tierra-firme* forest, as well as forest type preference, were determined along transects, while an index of secondary forest preference was calculated from transects by boat through secondary and successional habitat. A phenological study of over 1800 woody trees was used to determine patterns of food availability and to compare dietary selection based on items identified during foraging encounters. The parrot assemblage showed niche differentiation both through indices of dietary overlap and habitat preference. Dietary width was broad for most species, although dietary items were not eaten in relation to their abundance indicating selection of preferred food types. Seeds and fruit featured prominently in the diet of most species, although a range of other items, including bark, insects and lichen, were also consumed. For all but one parrot dietary breadth was not correlated with claylick use but for the most part increased with species of trees fruiting. Since animals faced with a range of toxins in their diet should have broad dietary breadth (a prediction of the toxin limitation hypothesis), this suggests against the consumption of clay to primarily counter dietary toxins. Instead, niche position (specifically the use of secondary and successional habitats) may be a better predictor of a species need for clay consumption.

## 5.2 INTRODUCTION

Dietary knowledge is fundamental for understanding species' niches, habits and roles in communities (Moegenburg and Levey, 2003, Munshi-South and Wilkinson, 2006). In southeastern Peru hundreds of individuals of up to 20 species of parrot consume clay daily from river bank claylicks (Chapter 2). These patterns are seasonal (Chapter 3) as are changes in abundance (Chapter 4).

Seasonal changes in local abundance patterns of parrots may be the result of seasonally available food resources within habitat mosaics (e.g. Ragusa-Netto, 2007). However, very little is know about the details of parrot diet in the wild (Koutsos et al., 2001). Some studies have identified plant species consumed in southeastern Peru (Gilardi, 1996), but no information exists on patterns of seasonal change in dietary breadth or how these are correlated with habitat preference, and in turn how they are related to claylick use.

Most part parrot species consume seeds and are considered important seed predators (Higgins, 1979, Galetti, 1992, Gilardi, 1996, Trivedi et al., 2004, Renton, 2006). In addition, most parrots consume at least some fruit (Galetti, 1997) and individual species are able to exploit a wide range of other food resources including flowers and nectar (Cotton, 2001, Raguso-Netto, 2006), insect larvae in galls (Martuscelli, 1994, Renton, 2006), termites (Sazima, 1989), leaves (Kristosch and Marcondes-Machado, 2001, Greene, 1999), carrion (Greene, 1999) and horse and cow dung (Ndithia and Perrin, 2006).

Claylick use differs between species (Chapter 3). The patterns of resource use of regular claylick user species versus non-user (or infrequent user) species could differ in various ways. For instance, claylick using species may utilise claylicks due to dietary deficiencies associated with plant availability in preferred habitat types (niche position). It is also feasible that claylick using avian species may utilise a narrower range of resources than non-users (niche breadth) given that clay binds dietary toxins (Gilardi et al., 1999) and given that mammal herbivores increase their dietary diversity when faced with a variety of chemically defended foods (a prediction of the detoxification limitation hypothesis (Marsh et al., 2006)). Furthermore, should clay bind dietary toxins then dietary width should be narrower during seasonal peaks of claylick activity.

In this study, I investigate the relationship between patterns of food resource use and claylick use among a lowland rainforest parrot assemblage in Tambopata, Peru. I examine the relationship between claylick dependence and a range of dietary and habitat variables.

### 5.2.1 Aim

To identify diet and dietary breadth, dietary shifts and food availability within a parrot assemblage in lowland Amazon rainforest of southeastern Peru and determine if any of these are related to claylick use. To achieve this I have the following objectives:

1. Determine tree species relative abundance and phenological patterns by season and forest types in order to determine patterns of potential food availability and seasonal change in diet

2. Identify the diets of individual species and determine community structure through dietary similarity

3. Identify correlates of claylick use (daily use and dependency) on a range of species specific (weight, density), dietary (niche breadth, niche position, niche overlap) and habitat (habitat preference) variables

4. Test predictions made by the toxin limitation theory; specifically whether dietary breadth decreases with claylick use

## 5.3 METHODS

### 5.3.1 Study site

The survey was conducted in the Tambopata National Reserve and associated buffer zone, as described in Chapters 3 and 4. Daily claylick use values are based on the mean values of use from the five Tambopata claylicks presented in Chapter 3.

### 5.3.2 Woody plant abundance and phenology

A total of 3,266 trees with diameter >10cm were marked with standard aluminium tags or marking tape in 30 plots of 10m x 100-200m long (5 ha total). Plots were located in *tierra-firme* forest, floodplain forest and successional forest at Refugio, Posada and TRC (Figure 5.1). These trees were used to calculate relative abundance of woody tree species within the lowland forest associated with the Tambopata River. A subset of 1,819 trees was monitored on a monthly basis for the presence of fruit and flower from January 2006 to December 2009 at Posada and Refugio. Monitoring was not possible for all plots every month, so results from all years are combined for the presentation of seasonal phenological patterns, recognising this may mask mast seed production events by certain species. Trees were identified by Percy Mario Nuñez of the Alwyn Gentry Herbarium, University of Cusco in 2008. By this time, 6% of the trees originally marked had died or been lost, and so not all trees for which phenological data were available were identified. Trees which died were not replaced.

### 5.3.3 Foraging records

Standardized foraging transects were conducted along 12 routes of two kilometres length from January 2008 to December 2009 at Refugio Amazonas, Posada Amazonas and TRC (Figure 5.1). Transects were conducted between 06h00 and 10h00 and from 15h00 to 18h00. During transects, all perched birds within 200m of the transect line were recorded along with the following information: species, group size, time and perpendicular distance. If birds were observed foraging, the following additional information was recorded: other birds foraging concurrently, tree type or identification information including diameter at chest height and total height, habitat type and part of the plant consumed. However, since encounter rate was low (0.2 group encounters per kilometre), supplementary information was taken on diet on an *ad-hoc* basis whenever foraging birds were observed.

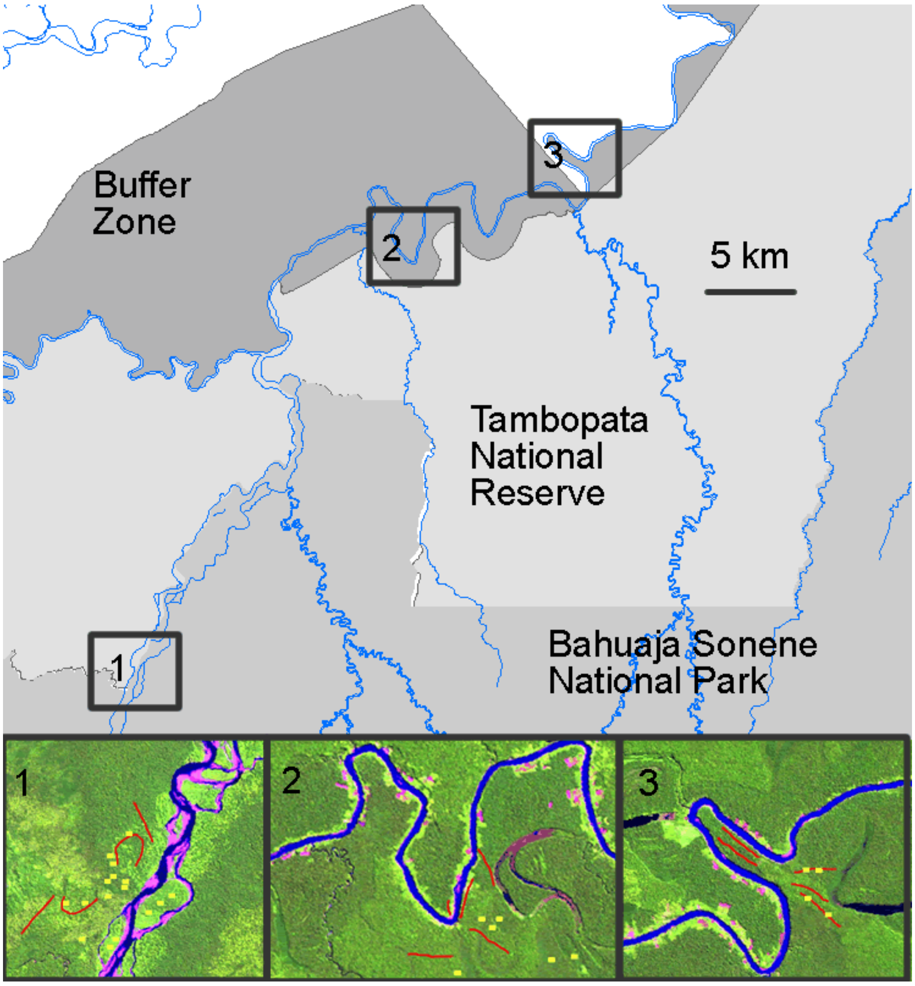

Figure 5.1: The foraging and phenology study area, showing the location of study sites as satellite image insets: 1 – TRC, 2 – Refugio, 3 – Posada. Foraging transect routes are red lines; phenology plot locations are yellow rectangles.

### 5.3.4 Indices of claylick use

For 13 parrot species, two principal indices of claylick use were measured: a standard daily mean based on five minute counts of birds on the lick (Brightsmith, 2004), where the mean daily feeding at five claylicks was calculated; and an index based on the proportion of local density (Chapter 3). The latter was calculated as the mean maximum number of birds observed on, or in the area of, the claylick divided by a local population estimate (bird density * area, with area defined by π * 10) from around the claylick complex and TRC. The mean of this proportion across claylicks was used as the measure of a bird species apparent need to use a claylick (hereon referred to as claylick dependence). This index is useful as it distinguishes rare species that may come from far away and hence appear common on the claylick, from a common species that visits less frequently from a smaller area.

Two secondary indices of claylick use were also used to correlate dietary variables: proportion of days seen at a claylick (a mean for all five Tambopata claylicks for which bird use data was available, Chapter 3), and also the reported proportion of claylicks visited by each parrot species across South America (Chapter 2).

### 5.3.5 Analysis overview

Broad phenological and foraging patterns are presented and analyzed using Spearman's ranked correlations among phenological patterns, diet, weight and daily claylick use. A community analysis of the parrot assemblage based on forage items is presented. Scores from the community analysis (Axis 1 and 2, used as indices of dietary overlap as the ordination groups species with similar diet), along with indices of habitat preference, density, dietary specialization, standard indices of dietary overlap, and seasonal change in abundance are then used as variables in correlation analysis to determine the relationship between habitat, diet and claylick use. The low number of samples (<13 parrots), which are also not independent due to phylogenetic relationships within the assemblage, suggests against multivariate regression analysis.

### 5.3.6 Parrot community analysis

A non-metric multidimensional scaling analysis (NMDS: CAP, Pisces Conservation Limited, 2002) was used to compare parrot community composition by diet at the plant genus level. Genus level was chosen as some food items could not be identified to species level, the software could not handle the number of identified species, and trees show many shared fruit and flower characteristics at the genus level. NMDS maximizes rank-order correlation between distance measures and distance in ordination space (Clarke, 1993). Analysis was run using the Sørensen index as the distance measure, a PCA (Principal Component Analysis) starting configuration (maximum of six axes and 200 iterations), and a final solution (number of axes) determined by minimising stress (McCune and Grace, 2002).

### 5.3.7 Dietary specialization

Nine indices of dietary specialization were calculated. Four values of dietary specialization based on plant components consumed were calculated for each parrot species as follows: the proportion of seed (including seed components e.g. embryo and endosperm); fruit pulp; flower; and entire fruit.

The proportion of non-ripe food items was calculated for all fruits and seed items consumed.

Each forage species was classified as either rare (<5/ha) or common (>5/ha) according to their occurrence in phenology plots. The forage species not recorded within phenology plots were classified as rare. The proportion of feeding observations on rare plant species was calculated for each bird species.

A standardized niche breadth index was calculated from the number of parrots observed feeding on each plant species consumed (Levins, 1968). Values close to 0 indicates dietary specialization and a value close to 1 indicates a broad diet.

Seasonal changes in diet were determined as the shared items between the wet (Nov–May) and dry seasons (Jun–Oct) as a proportion of all food items consumed.

Finally, a simple ratio of number of species as a proportion of all foraging events was calculated. This ratio was also used as a monthly measure of dietary breadth in relation to phenological patterns.

### 5.3.8 Niche overlap

Niche overlap (as a measure of potential competition) may influence claylick use as differential competitive abilities among species in the assemblage for shared resources might influence claylick use by forcing less competitive species to consume more toxic foods (and be greater claylick users). One would also expect species with a similar diet to show similar patterns of claylick use or dependency.

In addition to the NMDS results (axes 1 and 2 of the community analysis), two measures of similarity, or niche overlap, in diets were calculated. Firstly, Hulbert's measure of niche breadth (L), which incorporates measures of resource abundance (Hurlbert, 1978), in this case the relative abundance of food trees. Analysis was conducted at the plant genus level. Resource abundance was calculated from genus presence in phenology plots. The index assumes a value of 0 when no resources are shared, a value of 1 when both species utilize each resource in relation to its abundance, and a value of >1 if each species utilizes certain resources more intensively than others and the utilization functions of the two species tend to coincide. This index produces values that are weighted by foraging on rare items. In addition, the more frequently used Morisita's niche overlap index was used to produce a standardized comparative index. For each bird species I determined the similarity in the food composition of its feeding records with all other bird species individually, then calculated its overall mean similarity across the parrot assemblage.

### 5.3.9 Abundance and habitat use

Habitat specialisation (niche position) may influence claylick use for a variety of reasons. Successional forest parrot species may show greater preference for claylick use due to dietary similarity, limited resource choice and thus dietary deficiencies. They may also use claylicks more due to habitat proximity to claylicks as stands of secondary and successional forests tend to be associated with meandering river channels and anthropogenic disturbance. *Tierra-firme* and *aguajal* specialists may not have as easy access to claylicks and the associated species may not (or take longer to) learn the benefits of clay consumption. To quantify the relative use of river edge and successional habitat I calculated a ratio of perched parrots along a 54 km section of river that was traversed by boat 116 times throughout the study period. The transect excluded 2 km river sections associated with claylicks (1 km either side of a claylick). The forest associated with the river edge was either natural successional habitat associated with river course meandering; successional forest resulting from small scale slash-and-burn agriculture; or small scale agricultural plots in different stages of regeneration. As sightings were visual only (due to motor noise) and hence dependent on parrot size, the number of birds was divided by species weight. This value was divided by bird density (see below) to create an index of successional habitat preference. All birds scoring greater than 0.8 on this index are listed as being associated with successional forest (Forshaw, 2006), apart from Blue-headed Parrot *P. menstruus* and Yellow-crowned Parrot *A. ochrocephala*, which scored lower.

All other factors being equal I would expect a positive correlation between density and claylick use. A regional density estimate was calculated for each species, as well as for each species by habitat and season (Chapter 4). Seasonal change in density was calculated between dry and wet season, as this may be related to seasonal changes in claylick use. A further measure of habitat preference was calculated to determine specialization away from successional forests, as the density ratio between *tierra-firme* and floodplain forest types.

## 5.4 RESULTS

### 5.4.1 Woody plant relative abundance

Of 3,266 trees in quadrats 3,087 were identified to species level, with 432 species belonging to 226 genera and 71 families. Botanical classification follows APG (2003). The three most common families were Arecaceae with 745 individuals belonging to 10 species, Fabaceae with 308 individuals belonging to 61 species and Moraceae with 293 individuals belonging to 40 species. The top 10 families accounted for 71% of plant species. Parrots fed on 37% of plant genera represented in the quadrats. Twenty seven families and 143 genera recorded in quadrats recorded no foraging events. The majority of these (111 genera) were represented by fewer than 10 individuals (<2 ind/ha). Parrots fed on eight families and 36 genera not recorded in quadrats, although several of these were not woody trees e.g. lianas (*Combretum* spp. *Clusia* spp.), vines (*Arrabidaea* spp.) and bamboo (*Guadua* sp.).

### 5.4.2 Patterns of fruit and flower availability

The three most common tree families where phenological patterns were monitored were proportional to that of the total number of trees identified: Arecaceae 372 individuals of 8 species, Moraceae 208 of 32 species and Fabaceae 184 of 47 species. The top 10 families accounted for 70% of identified species. Trees were observed 47, 398 times during the course of the survey, however 603 of the +1800 trees were never registered with fruit or flower, so phenological patterns are based on the remaining 1,214 (30,051 observations). Mean fruit availability (proportion of occasions a tree was checked and had fruit) tended to be higher in floodplain forest compared to *tierra-firme* (median, interquartile range FP: 0.09, 0.05 - 0.23, TF: 0.08, 0.04 – 0.19; U = 369701, Z = -1.9, $p = 0.06$). A greater proportion of trees had flowers in the dry season (dry: 0.1, 0.07 – 0.2; wet: 0.08, 0.07 – 0.13; U = 1388498, Z = -10.1, $p < 0.001$), while fruit presence was greater in the wet season (dry: 0.13, 0.1 – 0.2; wet: 0.15, 0.08 – 0.3; U = 1540507, Z = -3.6, p < 0.001). Proportion of fruiting trees per month between habitats was highly correlated ($r_s$ = 0.9, p < 0.001, n =12). A peak in flowering in September proceeded the peak period in fruit availability from October to March (Figure 5.2).

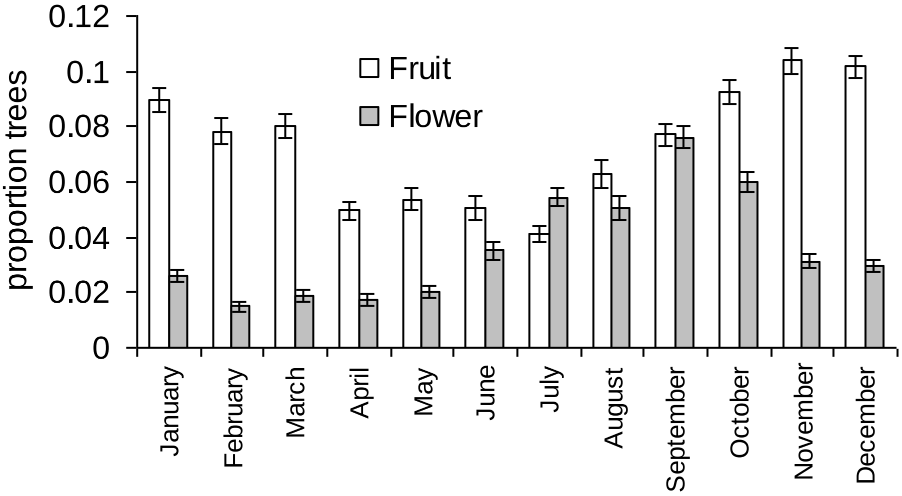

Figure 5.2: Phenological patterns for trees in plots at Refugio and Posada: the mean ± s.e. proportion of 1214 marked trees with fruit or flower per month for the period 2006-2009.

### 5.4.3 Foraging events

A total of 758 standardized surveys (1,468 km) were conducted over the sampling period. Thirteen species of parrots were encountered foraging during 285 encounters. There was a significant difference in foraging encounters per kilometre between dry season, June to October, and wet season, November to May (median encounter rate, interquartle range for dry season: 0, 0 – 0.5, wet: 0, 0 - 0.3; U = 65662, Z = -2.5, $p$ = 0.01). There were no differences in foraging encounters per kilometre between years (U = 66208, Z = -1.3, $p$ = 0.2) or between *tierra-firme* and floodplain forest types (U = 68063, Z = -1.6, $p$ = 0.1). There was a trend for the seasonal differences in encounter rates between season to be more pronounced in floodplain than in *tierra-firme* habitat (floodplain: U = 15574, Z = -1.87, $p$ = 0.06; *tierra-firme*: U = 17325, Z = -1.6, $p$ = 0.1).

The total number of foraging encounters for the survey period, including incidental encounters, was 1,469 groups of 16 species of parrots, of which 8.5% were multi-species groups. A total of 291 (20%) encounters were of species feeding on the observed tree where feeding had been observed previously, resulting in 1,178 independent observations. Only these independent observations were used for dietary breadth calculations and other correlations. Mealy Parrot were encountered most often (196 events), followed by White-bellied Parrot (190) and Scarlet Macaw (178), while Blue-headed Macaw *Primolius couloni*, Dusky-billed Parrotlet *Forpus sclateri* and Red-bellied Macaw *Orthopsittaca manilata* were recorded on three or fewer occasions. Feeding encounters were recorded on 49 families, 129 genera and 204 species of plant (Appendices 1a and 1b). Seven encounters were recorded on termites *Nasutitermes corniger* (Isoptera: Termitidae: Nasutitermitinae), by six species of parrot. White-bellied Parrot was observed feeding on ants *Crematogaster* sp. on one occasion. Blue-and-yellow Macaw *A. ararauna* and Red-and-green Macaw *A. chloropterus* were observed feeding on the lichen *Marchantia* (Marchantiaceae) on the bark of the emergent tree *Bertholletia excelsa*. Black-capped Parakeet *P. rupicola* was observed feeding on insect larvae of an undetermined species in leaf galls on two occasions. Six parrot species were recorded feeding on bark or dead wood of various tree species, comprising 1.1% (n = 13) of the total feeding encounters. The five most commonly consumed plant species were *Euterpe precatoria* Arecaceae (n = 156 encounters), *Bertholletia excelsa* Lecythidaceae (n = 95), *Ochroma pyramidale* Bombacaceae (n = 88), *Inga alba* Fabaceae (n = 63), *Cecropia sciadophylla* Urticaceae (n = 48).

Seeds (including seed parts e.g. endosperm and embryo) formed the major component of the plant part eaten by the parrots (35%, n = 572), followed by fruit pulp (31%), flower parts (18%), and entire fruit (14%). Leaves, bark and insects accounted for the remaining 2%. Seeds formed the largest proportion of plant part consumed for eight species (Blue-headed Parrot (47%), Blue-and-yellow Macaw (63%), Mealy Parrot (55%), Orange-cheeked Parrot (64%), Red-and-green Macaw (53%), Scarlet Macaw (57%), White-bellied Parrot (34%), Yellow-crowned Parrot (35%)); flower formed the major plant part consumed for four species (Chestnut-fronted Macaw (54%), Cobalt-winged Parakeet (41%), Dusky-headed Parakeet (48%) and White-eyed Parakeet (54%)); while for Black-capped Parakeet fruit pulp formed the largest proportion (39%). Larger species consumed a larger proportion of seeds in their diet ($r_s = 0.64$, $p = 0.02$, n = 13). Smaller species tend to consume more flowers ($r_s = -0.54$, $p = 0.06$, n = 13). There was no correlation between weight and proportion pulp ($r_s = 0.28$, $p = 0.35$, n = 13). Larger species consumed more unripe fruit and seeds than smaller species ($r_s = -0.61$, $p = 0.03$, n = 13).

### 5.4.4 Dietary breadth

There was no correlation between body mass and dietary breadth ($r_s = 0.12$, $p = 0.7$, n = 13). Dietary breadth (Levin's) was nearly positively correlated with the proportion of claylicks used in South America ($r_s = 0.54$, $p = 0.06$, n = 13 species).

For the nine species where more than 30 foraging events were encountered, Blue-headed Parrot *P. menstruus* had the broadest diet (Levin's = 0.55; preferred food species *Inga alba* recorded 15% of all foraging events) and Cobalt-winged Parakeet *B. cyanoptera* had the narrowest diet (Levin's = 0.24; 35% of all foraging events on *Ochroma pyramidale*). Sufficient encounters (>30) were obtained for ten parrot species to examine month by month simple dietary breadth change. An increase in dietary breadth was correlated with increased flower or fruit availability for six of the ten parrot species (Table 5.1). Dietary breadth was positively correlated with mean daily claylick use for just one species at the monthly level, White-bellied Parrot *P. leucogaster* (Table 5.1, $r_s = 0.81$, $p < 0.01$, n = 12).

Table 5.1: Correlation matrix of an index of simple dietary breadth (number of genera / number of foraging events) calculated for each month with proportion of trees with fruit (fruit availability), flower (flower availability) and index of mean daily claylick use. n = 12 months. $r_s$ = correlation coefficients. Significant results ($p < 0.05$) are presented in **bold**.

| | Flower availability | | Fruit availability | | Mean daily claylick use | |
|---|---|---|---|---|---|---|
| | $r_s$ | P | $r_s$ | p | $r_s$ | P |
| Black-capped Parakeet | 0.33 | 0.30 | 0.64 | **0.03** | 0.24 | 0.46 |
| Blue-headed Parrot | 0.70 | **0.01** | 0.30 | 0.34 | 0.44 | 0.15 |
| Blue-and-yellow Macaw | 0.16 | 0.61 | 0.52 | 0.08 | 0.41 | 0.19 |
| Chestnut-fronted Macaw | 0.25 | 0.43 | 0.32 | 0.30 | 0.11 | 0.74 |
| Cobalt-winged Parakeet | -0.32 | 0.32 | 0.31 | 0.33 | -0.24 | 0.46 |
| Mealy Parrot | 0.65 | **0.02** | 0.13 | 0.69 | 0.22 | 0.49 |
| Orange-cheeked Parrot | 0.19 | 0.65 | -0.79 | **0.02** | 0.03 | 0.95 |
| Red-and-green macaw | 0.78 | **<0.01** | -0.22 | 0.50 | -0.20 | 0.54 |
| Scarlet Macaw | 0.48 | 0.11 | 0.13 | 0.69 | -0.10 | 0.75 |
| White-bellied Parrot | 0.62 | **0.03** | 0.63 | **0.03** | 0.81 | **<0.01** |

### 5.4.5 Dietary overlap

Species with an association with successional forest types (White-eyed Parakeet *A. leucophthalmus*, Dusky-headed Parakeet *A. weddellii*, Chestnut-fronted Macaw *A. severus* and Yellow-crowned Parrot *A. ochrocephala*) were grouped closely in the community analysis based on plant genera consumed (Figure 5.3). Cobalt-winged Parakeet *B. cyanoptera* was not as closely associated with these species as might be expected by diet which was heavily influenced by *Ochroma pyramidale* (an indicator species of successional forest). The large macaws formed a loose group, while most other species were not closely associated, suggesting a large degree of niche differentiation at the dietary level.

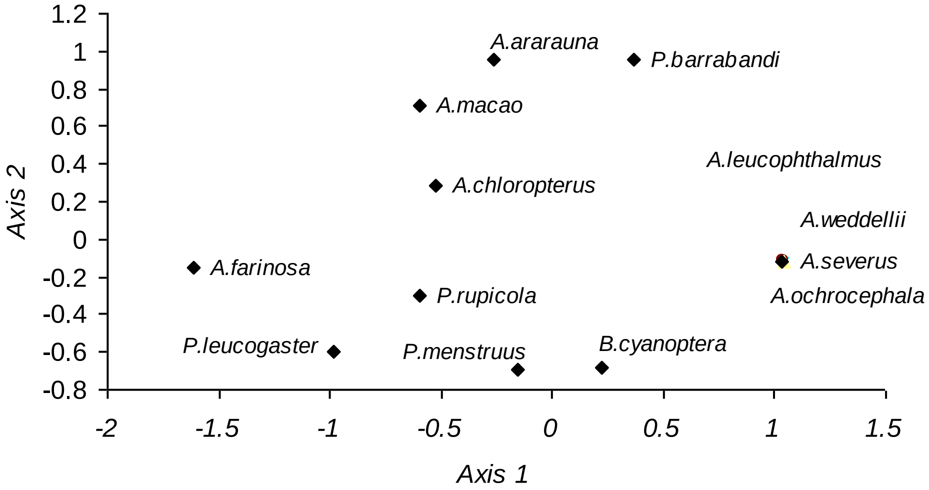

Figure 5.3: Non-metric multidimensional scaling (NMDS) visual interpretation of scaled distances (Axis 1 v Axis 2) for 13 species of parrot based on similarity of diet at the plant genus level (STRESS = 0.09).

### 5.4.6 Density and habitat preference

Dusky-headed Parakeet *A. weddellii* and Chestnut-fronted Macaw *A. severus* were the species most associated with successional forest, while Orange-cheeked Parrot *P. barrabandi*, Mealy Parrot *A. farinosa* and White-bellied Parrot *P. leucogaster* showed the lowest levels of successional habitat association (Appendix 5.2). Species with high successional forest association consumed fewer seeds ($r_s = -0.6$, $p = 0.03$, n =13). The index of successional forest use was positively correlated with Hurlbert's niche overlap ($r_s = 0.6$, $p = 0.02$, n =13), as plant species dominating successional forest are rare over the wider landscape (they formed a small proportion of the trees in phenology plots).

The three species associated with floodplain forest (with a high floodplain:*tierra-firme* density ratio; Appendix 5.2) were Cobalt-winged Parakeet *B. cyanoptera,* Yellow-crowned Parakeet *A. ochrocephala* and Black-capped Parakeet *P. rupicola*, while species most strongly associated with *tierra-firme* forest were Scarlet Macaw *A. macao,* Orange-cheeked Parrot *P. barrabandi* and White-bellied Parrot *P. leucogaster.* There was a negative correlation between this index and the proportion of seeds consumed ($r_s = -0.64$, $p = 0.02$, n =13), suggesting that species associated with floodplain consume fewer seeds than *tierra-firme* species.

Of the dietary variables, bird density was correlated only with proportion of whole fruit consumed ($r_s = 0.71$, $p = 0.007$, n =13). However, seasonal change in abundance between dry season and wet season was correlated with the proportion of rare species in the diet ($r_s = 0.55$, $p = 0.05$, n =13), suggesting that a degree of seasonal movement may be driven by phenological patterns of rarer plant species.

### 5.4.7 Dietary and habit correlates of claylick use

Daily claylick use was not correlated with any of the 18 habitat or dietary variables. Claylick dependence was negatively correlated with NMDS Axis 2 and positively correlated with the index of successional forest use, and showed a weak positive association with Hurlbert's L (Table 5.2). Both Axis 2 and Hurlbert's L are measures of dietary overlap, one at the genus level, and the other in relation to use of rare species, indicating a multi-tiered differentiation in dietary selection in relation to claylick use.

Table 5.2: Dietary and habitat correlations (Spearman's) of claylick use. Data used in correlation tests are available in Appendix 5.2. Significant results are indicated in bold. n = 13 species.

| | Daily use | | Dependence | |
|---|---|---|---|---|
| | $r_s$ | p | $r_s$ | p |
| NMDS Axis1 | 0.02 | 0.94 | 0.38 | 0.20 |
| NMDS Axis2 | -0.15 | 0.63 | -0.67 | **0.01** |
| Body weight | 0.19 | 0.54 | -0.36 | 0.22 |
| Levin's | 0.03 | 0.92 | 0.20 | 0.51 |
| Simple diet width | -0.39 | 0.19 | -0.06 | 0.86 |
| Proportion flower | -0.19 | 0.54 | 0.43 | 0.14 |
| Proportion pulp | -0.25 | 0.41 | -0.50 | 0.09 |
| Proportion seed | -0.01 | 0.97 | -0.43 | 0.14 |
| Proportion whole | 0.00 | 1.00 | -0.17 | 0.59 |
| Proportion unripe | -0.11 | 0.72 | -0.34 | 0.26 |
| Hurlbert's L | 0.00 | 1.00 | 0.52 | 0.07 |
| Morisita | -0.25 | 0.41 | 0.04 | 0.89 |
| Population density | 0.21 | 0.49 | -0.43 | 0.14 |
| Seasonal change in diet | 0.04 | 0.90 | -0.24 | 0.44 |
| Index of successional forest use | 0.45 | 0.13 | 0.62 | **0.02** |
| Seasonal change in abundance | -0.06 | 0.85 | 0.03 | 0.92 |
| Ratio: Floodplain:Terra-firme | 0.28 | 0.35 | 0.43 | 0.14 |
| Proportion rare plants in diet | 0.18 | 0.55 | -0.15 | 0.62 |
| Mean proportion of days observed at five claylicks | 0.58 | **0.04** | 0.36 | 0.22 |
| Global proportion claylicks used | 0.49 | 0.09 | 0.52 | 0.07 |
| Mean daily claylick use | | | 0.30 | 0.32 |
| Claylick Dependence | 0.30 | 0.32 | | |

## 5.5 DISCUSSION

### 5.5.1 Phenology and food availability

The number of trees recorded in site studies from nearby Manu is over 1,000 (Pitman et al., 2002). In our study, of the over 400 species of trees identified, parrots consumed 37%. This suggests that there are potentially over 370 plant species available as food sources to the parrot assemblage. That we only identified 204 of these in a multi-year study highlights the difficulty of gathering data on the parrot family in the Neotropical environment. Rare species were under represented in this study, and would need to be the focus of targeted studies in order to gather the information undoubtedly crucial to their survival.

The phenological patterns identified here were expected – tropical environments with dry and wet seasons frequently record peaks in fruit availability during wet periods (Bjork, 2004, Smythe, 1970). The current paradigm is that climate influences plant phenological patterns whereby seeds are produced while resources are available to do so, thus creating abundant seasonal food availability for frugivorous species, during which time birds nest so they have food to feed their young (Bissonette and Storch, 2007). During these times in southeastern Peru claylick use is high and are further correlated with local changes in parrot relative abundance (Brightsmith, 2006). Seasonal changes in abundance may be related to seasonal higher abundance of potential food resources in floodplain forest types.

### 5.5.2 Broad dietary patterns: comparisons with other studies

This study shows various parallels with Gilardi's (1996) study of parrot foraging ecology, which revealed that these birds were exploiting a relatively open niche which provided them with rich resources, even in lean times. Parrots were rarely associated with other birds and mammals foraging in the same tree. Parrots ate seeds, fruits, flowers, leaves, and bark, and insect larvae. I also show that parrots are selective in their diet, ignoring certain common plant species, while actively seeking out selected rarer species. Military Macaws *Ara militaris* have been shown to be selective regarding their food choice in the wild and also do not eat plants in proportion to their abundance (Contreras-Gonzalez et al., 2009). Like Gilardi (1996), I found that body size was a poor predictor of dietary similarity. However, body size does explain a degree of niche partitioning, with larger species consuming more seeds and more unripe plant items than smaller species, which extend their dietary niche into flowers.

Most studies conducted on Neotropical parrot diet to date report a range of food items consumed and suggest broad dietary width (e.g. Matuzak et al., 2008). Our study shows that Scarlet Macaw *Ara macao* have a wide dietary breadth (73 plant species consumed). Dietary breadth for this species may be wider in southeastern Peru compared to central American locations: Scarlet Macaws have been reported to consume 52 food species in the Amazonian rainforest of Peru (Gilardi, 1996) but only 28 food species in tropical dry forest of Costa Rica (Renton, 2006). Adult Scarlet Macaws observed over a five month period in Costa Rica were recorded feeding on 15 plant species from 12 families, with seeds forming 76% of the diet (Vaughan et al., 2006). Scarlet Macaws in Costa Rica feed on seeds, fruits, leaves, flowers and/or bark of 43 plant species including exotic species introduced as crops (Nemeth and Vaughan, 2004).

Blue-and-yellow Macaw *Ara ararauna* show a fairly broad dietary width in this study – feeding on over 30 plant species, but was recorded feeding on just ten different species in a Cerrado fragment in Brazil during observations carried out over one year, where *Vatairea macrocarpa* (Leguminosae) formed 68% of the feeding events (Ragusa-Netto, 2006). Mealy Parrot *Amazona farinosa* was recorded feeding on 33 species in Guatemala (Bjork, 2004), while we recorded 78 species.

It is not clear from these previously mentioned dietary studies what proportion of the available plant species are being consumed – the western Amazon has high plant species richness (Pitman et al., 2008) and so greater dietary width is likely correlated to this. I hesitate to link claylick use to greater dietary breadth due to lower parrot species richness at Ecuadorian claylicks (Chapter 2), where the greatest plant species richness in the Amazon is known to occur (Pitman et al., 2002) and where if dietary width and geophagy are linked one would predict at least similar species richness at Ecuadorian claylicks to those of southeastern Peru.

The abundant availability of flowers and fruits in the gallery forest of the southern Pantanal, Brazil, may account for the presence of large parrot populations where seven species of parrot were observed feeding on 29 different species of woody plant (Ragusa-Netto and Fecchio, 2006). Similarly, a wide variety of habitats in southeastern Peru, with high associated plant species richness, coupled with niche partitioning among the parrot family, allows for a very species rich parrot assemblage.

### 5.5.3 Toxin delimitation and claylick use: for and against

The detoxification limitation hypothesis (Freeland and Janzen, 1974, Dearing and Cork, 1999) suggests that the ability of generalist herbivores to eliminate plant secondary metabolites (PSMs) largely determines which plants, and how much, they can eat. It is a difficult hypothesis to formally test, requiring an understanding of the metabolic pathways that lead to toxin elimination. However, I am able to discuss the implications of these finding in the light of the prediction about animal feeding offered by the detoxification limitation hypothesis:

1. Feeding rates depend on the rates at which herbivores can detoxify PSMs so the herbivore will need to alter its rate of feeding with changing concentrations of a PSM in the food to keep the rate of ingestion of the PSM stable (Marsh et al., 2006).

2. Specialist herbivores should be better at detoxifying the PSMs they encounter than should generalists. Specialist herbivores rely on few plants for most of their food, whereas generalist herbivores tend to eat many different plants, even when one is abundant (Marsh et al. 2006).

3. As a consequence of prediction 2, the ability of a herbivore to deal with toxins determines dietary width and how much it can eat (Sorensen and Dearing, 2003).

Few studies of Neotropical bird groups feeding rates, coupled with a lack of the intricate knowledge needed to understand how birds deal with toxins, make it difficult to comment on the first prediction in relation to how feeding rates compare across families. At the very least, the number of birds foraging per hour is correlated with other canopy frugivores – guans and toucans, suggesting that parrots do not have to spend longer foraging in order to balance toxin loads (Lee unpublished data). All parrot species studied here had broad diets, consistent with the prediction that species faced with a range of dietary toxins exhibit broad dietary width. Gilardi (1996) showed that plant materials eaten by parrots were generally rich in protein, lipid, essential minerals, and often potentially toxic chemicals, that no macaws avoid toxic plants, and that one species (*A. macao*) selected foods that were significantly more toxic than many foods that they avoided. The parrot family are also regarded as specialists with regards seed predation – no other Neotropical bird family competes (Juniper and Parr, 1998). Thus for the parrot family as a whole, there is support for predictions 2 and 3.

Extending the reasoning of the hypothesis, if we substitute ‘generalist’ with parrot species that use claylicks less frequently and ‘specialist’ by more frequent claylick users (due to the ability of the clay to neutralize toxins) then we can re-examine prediction 3. Dietary breadth was not correlated with claylick dependence for the family as a whole, suggesting then that toxins are either not a leading explanatory variable, or that the toxin limitation theory does not hold for the parrot family. In contrast, that dietary breadth at the seasonal level was only correlated (positively) with mean daily claylick use for one species suggests against the hypothesis that claylick use allows species to eat more food items normally protected with dietary toxins, proposed by Diamond (1999). It also suggests against the toxin delimitation theory, where negative correlations would have been expected, thus implying that parrot species are physiologically able to deal with the diets they choose.

Where the toxin delimitation hypothesis is accounted for is in the dietary breadth for Scarlet Macaw *A. macao* chicks, which is much lower than that recorded for adults (Renton, 2006, Brightsmith unpubl. data). In southeastern Peru, as much as 80% of crop samples from *A. macao* chicks consists of clay (Brightsmith and Cornejo, 2009). As such, macaws may thus be counteracting toxins in food sources rich in protein and fat from a smaller range of plants that are also chemically well defended. Thus, background levels of geophagy may be partially explained by dietary deficiencies, while toxin adsorption may explain a degree of seasonal changes in claylick use, which are strongly correlated with breeding season (Brightsmith and Cornejo, 2009). Developing chicks may not have the capacity to deal with dietary toxins as do adult parrots, but rapidly growing chicks would also have a high nutrient demand.

I also show that dietary width increases seasonally in proportion to available food resources for over half the species for which data was available. The data show that seasonal changes in abundance are more correlated with the fruiting of rare species associated with floodplain forests than with claylick use. Claylick use instead was more associated with species preferring successional forest. Plants invest more resources in defending leaves, and presumably other plant parts, that will be longer lasting (Coley and Barone, 1996). Plants' allocation of resources to chemical defence may be at the expense of growth (Herms and Mattson, 1992). Possibly related to this is that the species *Ochroma pyramidale, Inga alba* and *Cecropia sciadophylla*, all associated with successional forest, were among the top five species where I recorded the greatest numbers of foraging encounters, and are also eaten by a range of other birds and mammals (Lee pers obs.). This suggests that the plant species assemblage in successional forest is most likely the least well chemically defended, arguing against the need to consume soils to protect against dietary toxins. Coupled with this, birds associated with secondary habitat consumed the lowest proportions of seeds. As such, I speculate that the narrower species richness of successional forest species is more likely to result in a nutrient deficient diet compared to species presented with a wider variety (of presumably better chemically protected) plant species from species rich mature floodplain and *tierra-firme* forests.

Gilardi (1996) concluded that macaws did not appear to make dietary selections based on mineral content. However, that parrots choose foods based on dietary needs is displayed in crop samples from Scarlet Macaw *Ara macao* chicks, where crop contents contained higher protein levels, fat levels and the macroelements calcium and magnesium than the average food plants (Brightsmith and Cornejo, 2009). A study of geophagy from southeastern Peru was able to rule out all the minerals except sodium as the primary cause of geophagy (Gilardi et al., 1999). Sodium is consistently low in all dietary components, while potassium is generally high (Brightsmith in press). The sodium levels of crop contents were nearly seven times the values in the average food, suggesting that the adults actively seek out sodium sources (Brightsmith and Cornejo, 2009) – and claylick soil is an important source of sodium (Powell et al., 2009).

It has previously been stated that claylick use may well be related to a variety of the reasons that best explain geophagy for different species in different parts of the world (Diamond et al., 1999). I caution against extrapolating reasons for geophagy across species and regions, and although claylick use does not appear to be related to diet for this assemblage of parrots in this part of the world, it by no means signifies that this applies to other parrot communities (or species) in other parts of the world.

### 5.5.4 Acknowledgements

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Appendix 5.1a: Foraging items of small parrots and parakeets from survey sites along the Tambopata river for the 2005-2009 period. F = flower, W = whole fruit, S = seed or seed parts, *P* = pulp, O = other, U = unknown, IN = insect.

| | *P. rupicola* | | | | | | | *B. cyanoptera* | | | | | | | *A. leucopthalamus* | | | | *A. weddellii* | | | | | *P. menstruus* | | | | | | *P. barrabandi* | | | *P. leucogaster* | | | | | |
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| | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| ANNONACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Oxandra xylopioides* | | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | | | 1 | | |
| APOCYNACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Rauwolfia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| ARECACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Euterpe precatoria* | | | | 12 | 3 | 1 | | | | | 4 | | | | 1 | 4 | | | | | 1 | | | | | 5 | | | | | 1 | | | | 32 | 6 | 3 | |
| *Iriartea deltoidea* | 8 | | | 1 | | | | 1 | | | 1 | | 2 | | | | | | | | | | | | | 1 | | | | | | | 4 | | | | | 1 |
| *Mauritia flexuosa* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Oenocarpus bataua* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Socratea exorrhiza* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| BIGNONIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Arrabidaea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | |
| *Mansoa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| BOMBACACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Chorisia insignis* | | | | | | | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Huberodendron swieteniodes* | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ochroma pyramidale* | 13 | | | 1 | | | | 29 | | | 1 | | | | 7 | | | | 8 | | | | | | | | | | | 1 | | | 1 | | | | | |
| BROMELIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Aechmea angustifolia* | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Streptocalyx* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| BURSERACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Protium sagotianum* | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| CARYOCARACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Caryocar pallidum* | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| CLUSIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Chrysoclamys ulei* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 9 | | 1 |

|  | *P. rupicola* |  |  |  |  |  |  | *B. cyanoptera* |  |  |  |  |  |  | *A. leucopththalamus* |  |  |  | *A. weddellii* |  |  |  |  | *P. menstruus* |  |  |  |  |  | *P. barrabandi* |  |  | *P. leucogaster* |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| *Clusia* |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 4 |  |  |
| *Moronobea coccinea* |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Symphonia globulifera* | 1 |  |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  |  |  |  |  |  | 15 |  | 1 | 1 |  |  |
| *Tovomita stylosa* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2 |  |  |
| COMBRETACEAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Combretum fruticosum* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Combretum laxum* |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Combretum sp* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |
| *Terminalia oblonga* |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |
| EBENACEAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Diospyros poeppigii* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| EUPHORBIACEAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Alchornea triplinervis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |
| *Croton lechleri* | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Drypetes gentryi* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |
| *Sapium glandulosum* |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Sapium ixiamasense* |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Sapium marmieri* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 2 |  |  |
| FABACEAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Abarema laeta* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |
| *Acacia loretensis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |
| *Apuleia leiocarpa* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |
| *Cedrelinga cateniformis* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  | 2 |  |
| *Dialium guianense* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Dipteryx micrantha* | 1 |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  | 1 |
| *Enterolobium barnebyanum* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 |  |  |  |  |  |  |  |  |  |  |  |
| *Erythrina* |  |  |  |  |  |  |  | 2 |  |  |  |  |  |  | 1 |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |

| | *P. rupicola* | | | | | | | *B. cyanoptera* | | | | | | | *A. leucopth-thalamus* | | | | *A. weddellii* | | | | | *P. menstruus* | | | | | | *P. barrabandi* | | | *P. leucogaster* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| *Erythrina poeppigiana* | | | | | | | | 2 | | | | | | | 9 | | | | 6 | | | | | | | | | | | | | | | | | | | |
| *Erythrina ulei* | | | | | | | | 1 | | | | | | | 5 | | | | 2 | | | | | | | | | | | | | | | | | | | |
| *Hymenaea oblongifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Inga* | | | | | | 1 | | | | | | | | | | | 1 | | | 1 | | 1 | | | | 1 | 2 | 1 | | | | | | | | | 2 | |
| *Inga alba* | | | | 2 | | | | | | | | | | | | 1 | | | | | | | | | 1 | 2 | 3 | | | | | | | | 2 | 2 | | |
| *Inga cinnamomea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Inga coriacea* | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | | | | | |
| *Inga edulis* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | 1 | | | |
| *Inga punctata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Machaerium* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Pterocarpus rohrii* | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 | | | | | |
| *Swartzia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Tachigali polyphylla* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| *Tachigali vasquezi* | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | |
| *Zygia corombosa* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| FLACOURTIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Laetia procera* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | |
| HUGONIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Roucheria punctata* | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| ICACINACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Leretia cordata* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| LECYTHIDACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Bertholletia excelsa* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 6 | 1 | | 1 | | |
| *Cariniana estrellensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Cariniana guianensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | |
| *Couratari guianensis* | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | |
| LORANTHACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

| | *P. rupicola* | | | | | | | *B. cyanoptera* | | | | | | | *A. leucopth-thalamus* | | | | *A. weddellii* | | | | | *P. menstruus* | | | | | | *P. barra-bandi* | | | *P. leucogaster* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| *Psittacanthus* | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| MALPIGHIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Byrsonima poeppigii* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | |
| *Mascagnia platyrachis* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| MALVACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Apeiba aspera* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | 2 | | |
| *Ceiba pentandra* | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| MARCGRAVIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Norantea guianensis* | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| MELASTOMATACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Miconia barbeyana* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| MELIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Guarea guidonia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| MENISPERMACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Anomospermum boliviana* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 | | | |
| MORACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum* | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum acutifolium* | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Brosimum acutifolium subsp obovatum* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Brosimum alicastrum* | | | | 2 | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum lactescens* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Castilla ulei* | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| *Ficus* | | | | | 1 | | 1 | | | | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus caballina* | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus coerulescens* | | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus guianensis* | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus insipida* | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | |

| | *P. rupicola* | | | | | | | *B. cyanoptera* | | | | | | | *A. leucopththalamus* | | | | *A. weddellii* | | | | | *P. menstruus* | | | | | | *P. barrabandi* | | | *P. leucogaster* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| *Ficus killipii* | | | | | 1 | 1 | | | | | | 1 | 7 | 1 | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| *Ficus mathewsi* | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus maxima* | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | | | | | | | | | | 1 | 1 | 1 | |
| *Ficus paraensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 4 | 1 |
| *Ficus perforata* | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus pertusa* | | | | | | | | | | | | 1 | 5 | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| *Ficus schultsi* | | | | | 1 | | | | | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | | | | 1 | | |
| *Ficus sphenophylla* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Ficus trigona* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Helianthostylis acuminata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| *Pseudolmedia* | | | | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 | |
| *Pseudolmedia laevigata* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 2 | | |
| *Pseudolmedia laevis* | | | | 2 | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | | | | | | | | |
| *Pseudolmedia macrophylla* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| MYRISTICACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Otoba glycicarpa* | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 2 | | | |
| *Otoba parvifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| OCHNACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ouratea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| RUBIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Calycophyllum spruceanum* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| RUTACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Zanthoxylum huberi* | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Zanthoxylum tambopatense* | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | |
| SAPINDACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sapindus saponaria* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| SAPOTACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

| | *P. rupicola* | | | | | | | *B. cyanoptera* | | | | | | | *A. leucopththalamus* | | | | *A. weddellii* | | | | | *P. menstruus* | | | | | | *P. barrabandi* | | | *P. leucogaster* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | In | L | P | S | W | U | F | In | L | P | S | W | U | F | P | S | U | F | O | P | S | W | F | O | P | S | W | U | F | P | S | F | O | P | S | W | U |
| *Chrysophyllum argentium* | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ecclinusa guianense* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| *Ecclinusa lanceolata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Pouteria* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | |
| *Pouteria procera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 2 | | |
| *Pouteria trilocularis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | 1 | | |
| STERCULIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pterygota amazonica* | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | |
| ULMACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Celtis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Celtis iguanaea* | | | | | | | | | | | | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | |
| *Trema micrantha* | | | | | | 2 | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| URTICACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cecropia* | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cecropia sciadophylla* | 1 | | | 1 | 1 | 3 | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | 1 | 1 | |
| *Cecropia tesmanni* | | | | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Coussapoa trinervia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| *Pourouma cecropiifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 3 | | 1 |
| *Pourouma cucura* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Pourouma guianensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Pourouma minor* | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 6 | | | 2 | 1 | | |
| *Pourouma mollis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | 1 | | |
| *Pourouma palmata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| VOCHYSIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Qualea grandiflora* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | |
| TERMITIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Termites* | | 1 | | | | | | | 2 | | | | | | | | | | | 1 | | | | | 1 | | | | | | | | | | | | | |

Appendix 5.1b: Foraging items of large parrots and macaws from survey sites along the Tambopata River for the 2005-2009 period. F = flower, W = whole fruit, S = seed or seed parts, *P* = pulp, O = other, U = unknown, IN = insect.

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| ANACARDIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Astronium graveolens* | | | 2 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Tapirira obtusa* | | | 5 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| ANNONACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Guatteria* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Oxandra xylopioides* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| APOCYNACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Aspidosperma megalocarpon muell* | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Tabernaemontana heterophylla* | | | | 2 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Tabernaemontana stenotachya* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ARECACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Euterpe precatoria* | | | 10 | 1 | 2 | | | 1 | | | | | 2 | | | | | | | | 3 | | 1 | 1 | | | | 14 | 4 | | 1 | | | | 3 | | | |
| *Iriartea deltoidea* | | | 1 | | | | | | | | | | | | | 1 | | | | | 1 | | 1 | 1 | | | | | | | 1 | | | | | | | |
| *Mauritia flexuosa* | 1 | | 1 | | | | | | | | | | 3 | | | | | | | | 3 | | | | | | | 5 | | | | | | | | | | |
| *Oenocarpus bataua* | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 2 | | | 1 | | | | | | | |
| *Oenocarpus mapora* | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | |
| *Socratea exorrhiza* | | | | | | | | | | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| BIGNONIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Jacaranda copaia* | | | | | | | | | | | | | | | | | | | | | 1 | 7 | | | | | | | 4 | | | | | | | | | |
| *Sparattosperma leucanthum* | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| BIXACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Bixa urucurana* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| BOMBACACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Huberodendron* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *swieteniodes* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ochroma pyramidale* | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | 2 | | | | | | | 15 | | | | | | |
| BORAGINACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cordia ucayalina* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | | | | | |
| BURSERACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Protium amazonicum* | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | |
| *Protium aracouchini* | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Protium rhynchophylium* | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Trattinickia rhoifolia var. Lancifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| CARYOCARACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Anthodiscus klugii* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | 1 | | | | | | | | |
| *Caryocar amygdaliforme* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | | |
| *Caryocar glabrum* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| CLUSIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Chrysoclamys ulei* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Symphonia globulifera* | 3 | | | 1 | | | | | | 4 | | | | | | | | | | | | | | | 6 | | | | 1 | | | 1 | | | | | | |
| COMBRETACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Terminalia oblonga* | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | | | | | |
| CUCURBITACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cayaponia macrocalyx* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 | 2 | | |
| *Favillea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Fevillea amazonica* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| EBENACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Diospyros poeppigii* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ELAEOCARPACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sloanea fragrans* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
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| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Sloanea guianensis* | | | | 3 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| EUPHORBIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Croton lechleri* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | | | |
| *Dalechampia stipulacea* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Drypetes gentryi* | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | |
| *Hevea brasiliensis* | | | | | | | | | | | | | | 2 | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Sapium glandulosum* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sapium ixiamasense* | | | | 1 | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| *Sapium marmieri* | | | 1 | 5 | | | | | | | | | | | | | | | | | | | | | | | | | 8 | | 1 | | | | | 1 | | |
| FABACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acacia loretensis* | | | | 2 | | | | | | | | | | | | | | | 1 | | | | | | 3 | 1 | | | 1 | | | | | 1 | | 2 | | |
| *Apuleia leiocarpa* | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Barbebydendron riedelii* | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | |
| *Caesalpinia apuleia* | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | |
| *Cedrelinga cateniformis* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Copaifera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Dialium guianense* | | | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | | | |
| *Dipteryx micrantha* | 1 | 1 | 2 | | | | | | | | | | 1 | | | | | | 1 | 1 | 5 | 3 | | 1 | | 1 | 1 | | | | | | | | | | | |
| *Enterolobium* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Enterolobium barnebyanum* | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Enterolobium cyclocarpum* | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Erythrina* | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | |
| *Erythrina poeppigiana* | | | | | | | | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | 3 | | | | | | |
| *Erythrina ulei* | | | | | | | 1 | | | | | | | | | | | | | | | | | | 1 | | 1 | | 1 | | | 2 | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
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| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Hymenaea courbaril* | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Hymenaea oblongifolia* | | | | 5 | | 1 | | | | | | | | | | | | | | | | 1 | 1 | | | | | | | 1 | | | | | | | | |
| *Inga* | | | | | 1 | | | | | | | | | 2 | | | 1 | | | | | | 1 | | | | | 1 | 1 | | | | | | | | | |
| *Inga acreana* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| *Inga alba* | | | 5 | 1 | | | | | | | | | 1 | | | | | | | | | 1 | 1 | | | | | 1 | 2 | | | | | | | | | |
| *Inga chartacea* | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | 1 | |
| *Inga edulis* | | | 2 | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 1 | 1 | | | | 1 | | | |
| *Inga punctata* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | | | | | 1 |
| *Inga semialata* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| *Parkia* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Parkia nitida* | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Parkia velutina* | | | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Schizolobium parahybum* | | | | | | | | | | | | | | | | | | | | | | 4 | | | | | | | | | 1 | | | | | | | |
| *Schwartzia* | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | |
| *Swartzia* | | | | | | | | | | | | | | 4 | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| *Swartzia cardiosperma* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Tachigali polyphylla* | | | | 5 | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Tachigali vasquezi* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| FLACOURTIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Casearia decandra* | | | 4 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 3 | | 2 | | | | | | | |
| *Laetia procera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| LAURACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ocotea cernua* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| LECYTHIDACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Bertholletia excelsa* | | | | | | | | | | | | | 1 | 15 | | 1 | 7 | | | 1 | 3 | 12 | 2 | | 1 | | 1 | 1 | 9 | | | | | | | | | |
| *Cariniana decandra* | 1 | | | | | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | 2 | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Couratari guianensis* | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | 1 | | | | | | | | | |
| *Eschweilera coriacea* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | 2 | | | | | | | |
| *Eschweilera tesmanni* | | | | 1 | | | | | | | | | | 1 | | | | | | | | 4 | | | | | | | 6 | | | | | | | | | |
| LOGANIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Strychnos asperula* | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| MALPIGHIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Byrsonima* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| *Byrsonima arthropoda* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Byrsonima poeppigii* | | | | | | | | | 1 | | | | | | | | | | | | 1 | 1 | 1 | | | | | | 1 | | | | | | | | | |
| *Mascagnia platyrachis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| MALVACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Apeiba aspera* | | | | | | | | | | | | | 1 | | | | | | | | 1 | 3 | | | | | | 1 | 1 | 1 | | | | | | | | |
| *Ceiba samauma* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| *Quararibea ochrocalyx* | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | | | 2 | | | | | | | | | |
| MARCGRAVIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Norantea guianensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| MARCHANTIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Marchantia* | | | | | | | | | | | | 1 | | | | | | | | 1 | | | | | | | | | | | | | | | | | | |
| MELIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cedrela odorata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Guarea pubescens* | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Trichilia pleeana* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| MENISPERMACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Anomospermum boliviana* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Anomospermum grandifolium* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| *Borismene japurensis* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| MORACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Brosimum acutifolium* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum acutifolium subsp obovatum* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum alicastrum* | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum guianense* | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brosimum lactescens* | | | 1 | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Castilla ulei* | | | 2 | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| *Clarisia racemosa* | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus* | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ficus pertusa* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | | | | |
| *Ficus trigona* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Helicostylis tomentosa* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pseudolmedia* | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | |
| *Pseudolmedia laevigata* | | | 2 | 4 | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | |
| *Pseudolmedia laevis* | | | 5 | 3 | 4 | | | 1 | | | | | | | | | 1 | | | | | 1 | 1 | | | | | | | | | | | | | | | |
| *Pseudolmedia macrophylla* | | | 1 | 4 | | 1 | | | | | | | | | | | | | | | 1 | | | | | | | 2 | 1 | | | | | | | | | |
| *Pseudolmedia rigida* | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sorocea pileata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| MYRISTICACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Otoba* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Otoba parvifolia* | | | 1 | 5 | 1 | | | | | | | | 2 | | | | | | | | 1 | 1 | | | | | | 3 | 3 | | | | | | | | | |
| MYRTACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Psidium guajava* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | |
| OLACACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Heisteria acuminata* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| OPILICIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochro-cephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Agonandra* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| POACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Guadua* | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | | | | | | 1 | | | | | |
| *Hilla ulei* | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | |
| SAPOTACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ecclinusa lanceolata* | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Guatteria acutissima* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pouteria* | | | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pouteria macrophylla* | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Pouteria paridy* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pouteria procera* | | | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pouteria trilocularis* | | | 1 | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| STERCULIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Byttneria* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Byttneria pescaprafifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Byttneria pescapriifolia* | | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | 2 | 1 | | | | | | | | |
| *Guazuma ulmifolia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Sterculia rugosa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| *Sterculia tessmannii* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Theobroma* | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| URTICACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cecropia sciadophylla* | 1 | | 1 | | 2 | | | | | | | | | | 2 | | | | | | | | | | | | | | | | 1 | | | | | | | |
| *Pourouma* | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | | | | | | |
| *Pourouma cecropiifolia* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 | | 1 | | | | | | | | |
| *Pourouma guianensis* | | | 1 | | | | | | | | | | | | | | | | | | 3 | | | | | | | 2 | | | | | | | | | | |

| | *A. farinosa* | | | | | | *A. ochrocephala* | | | *A. ararauna* | | | | | | | *A. chloropterus* | | | | | | | | *A. macao* | | | | | | | *A. severus* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | O | P | S | W | U | F | P | S | F | L | O | P | S | W | U | F | In | L | O | P | S | W | U | F | L | O | P | S | W | U | F | L | O | P | S | W | U |
| *Pourouma minor* | | | 5 | 2 | | | | 1 | | | | | | | | | | | | | 1 | 2 | 2 | | | | | | 1 | | 1 | | | | | | | |
| *Pourouma mollis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| *Pourouma palmata* | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| VOCHYSIACEAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Qualea grandiflora* | | | | | | | | | | | | | | | | | | | | | | 5 | | | | | | | 2 | | | | | | | | | |
| *Qualea paraensis* | | | | 3 | | | | | | | | | | | | | | | | | | 3 | | | | | | | 1 | | | | | | | | | |
| TERMITIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Termites* | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | | | | 2 | | | | | | | | | | | |

Appendix 5.2: Correlates of claylick use – habitat and dietary variables used in the correlation analysis presented in Table 5.2.

| Variables:<br>Species: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *P. rupicola* | 0.60 | 0.30 | 75 | 0.37 | 0.45 | 0.18 | 0.39 | 0.26 | 0.13 | 0.42 | 33.7 | 0.02 | 8.09 | 0.31 | 0.04 | 0.83 | 2.38 | 0.38 | 0.21 | 39.81 | 0.70 | 0.43 |
| *P. menstruus* | 0.16 | 0.70 | 251 | 0.55 | 0.69 | 0.03 | 0.32 | 0.47 | 0.16 | 0.37 | 2.5 | 0.01 | 2.84 | 0.11 | 0.16 | 0.68 | 1.51 | 0.32 | 0.48 | 162.65 | 2.40 | 0.79 |
| *A. ararauna* | 0.26 | 0.96 | 1,125 | 0.32 | 0.48 | 0.10 | 0.21 | 0.63 | 0.03 | 0.74 | 15.2 | 0.01 | 0.37 | 0.15 | 0.04 | 0.71 | 1.18 | 0.75 | 0.13 | 58.55 | 0.50 | 0.29 |
| *A. severus* | 1.04 | 0.12 | 343 | 0.27 | 0.34 | 0.54 | 0.15 | 0.28 | 0.02 | 0.41 | 69.2 | 0.02 | 0.18 | 0.16 | 3.32 | 0.94 | 1.58 | 0.71 | 0.34 | 86.43 | 32.90 | 0.58 |
| *B. cyanoptera* | 0.22 | 0.69 | 56 | 0.24 | 0.36 | 0.41 | 0.11 | 0.18 | 0.29 | 0.23 | 66.8 | 0.01 | 11.59 | 0.30 | 0.87 | 0.65 | 4.30 | 0.55 | 0.25 | 176.20 | 5.35 | 0.55 |
| *A. weddellii* | 1.04 | 0.12 | 108 | 0.51 | 0.44 | 0.48 | 0.03 | 0.32 | 0.08 | 0.10 | 59.0 | 0.02 | 0.66 | 0.17 | 5.35 | 0.80 | 2.11 | 0.41 | 0.43 | 130.15 | 28.05 | 0.63 |
| *A. farinosa* | 1.61 | 0.15 | 626 | 0.44 | 0.40 | 0.03 | 0.32 | 0.55 | 0.09 | 0.46 | 3.8 | 0.05 | 14.74 | 0.28 | 0.01 | 0.79 | 2.21 | 0.39 | 0.42 | 294.59 | 1.80 | 0.63 |
| *P. barrabandi* | 0.37 | 0.95 | 140 | 0.36 | 0.60 | 0.13 | 0.16 | 0.64 | 0.06 | 0.53 | 20.0 | 0.01 | 1.00 | 0.22 | 0.00 | 0.64 | 0.96 | 0.26 | 0.34 | 49.00 | 4.00 | 0.59 |
| *A. chloropterus* | 0.52 | 0.29 | 1,214 | 0.33 | 0.42 | 0.06 | 0.25 | 0.53 | 0.11 | 0.61 | 14.9 | 0.01 | 2.17 | 0.30 | 0.22 | 0.91 | 1.58 | 0.69 | 0.48 | 181.99 | 1.40 | 0.64 |
| *A. macao* | 0.60 | 0.71 | 1,015 | 0.49 | 0.42 | 0.08 | 0.24 | 0.57 | 0.07 | 0.62 | 9.6 | 0.03 | 1.74 | 0.21 | 0.03 | 0.93 | 0.81 | 0.49 | 0.24 | 59.13 | 0.60 | 0.42 |
| *P. leucogaster* | 0.98 | 0.60 | 158 | 0.27 | 0.40 | 0.24 | 0.31 | 0.34 | 0.11 | 0.45 | 7.1 | 0.04 | 11.03 | 0.33 | 0.01 | 0.91 | 1.01 | 0.45 | 0.09 | 10.43 | 0.30 | 0.21 |
| *A. leucopthalma* | 1.04 | 0.12 | 155 | 0.44 | 0.42 | 0.54 | 0.18 | 0.28 | 0.00 | 0.76 | 46.7 | 0.02 | 0.96 | 0.36 | 0.52 | 0.86 | 1.59 | 0.41 | 0.12 | 145.78 | 9.90 | 0.48 |
| *A. ochrocephala* | 1.03 | 0.12 | 440 | 0.60 | 1.00 | 0.04 | 0.33 | 0.35 | 0.20 | 0.58 | 3.9 | 0.10 | 1.03 | 0.00 | 0.04 | 0.47 | 3.17 | 0.36 | 0.32 | 39.89 | 9.70 | 0.67 |

Variables: 1 NMDS results Axis1; 2 NMDS results Axis2; 3 Weight; 4 Levin's dietary breadth; 5 Simple diet width; 6 Proportion of flowers in diet; 7 Proportion pulp; 8 Proportion seed; 9 Proportion whole; 10 Proportion unripe; 11 Hurlberts L – measure of dietary overlap; 12 Morisita measure of dietary overlap; 13 Density (ind / km$^2$); 14 Seasonal change in diet; 15 Index of successional forest use; 16 Seasonal change in abundance; 17 Habit Ratio (density in Floodplain:Terra-firme); 18 Proportion rare plants in diet; 19 Mean proportion of days observed at five claylicks; 20 Mean daily claylick use (complex and TRC); 21 Claylick Dependence; 22 Proportion of claylicks used in South America;

# Chapter 6: Claylicks and people: conservation status and the impacts of tourism

## 6.1 SUMMARY

Individual macaw claylicks in southeastern Peru may be worth as much as $100,000 according to ecotourism operators in the region, with the potential for earning up to $50 per tourist per visit, excluding services such as transport, food and accommodation. This gives a maximum earning potential for surveyed claylicks of the Manu/Tambopata area of US$ 2.25 million, although real value is probably half this. Although claylicks are an integral part of ecotourism tours to southeastern Peru, fewer than 34% are formally protected by their location in national parks or other state protected areas. When including ecotourism and conservation concessions, 60% of the claylicks surveyed are protected. Ecotourism is one of Tambopata's top five most important economic activities and is experiencing high annual growth, but at the time of writing there were no formal protected area guidelines for the control of tourist behaviour or boat traffic around parrot claylicks. Although parrots appeared to have habituated to boat presence around one claylick and no differences in feeding are recorded in situations where tourists use blinds, boat encroachment to feeding birds and visitation at blinds beyond their capacity (or non-use of blinds) impact bird feeding behaviour. Based on bird reactions and feeding patterns in the presence of boats and tourists, we advocate a minimum viewing distance of 100m by boats within protected areas where birds are otherwise habituated to boat presence, and the use of blinds for viewing claylick activity. Tour operators were unanimous in their response that macaw claylicks should have some degree of state protection and claylicks may be better protected by encouraging ecotourism concessions around them.

## 6.2 INTRODUCTION

All available evidence indicates that riverside claylicks are very important in the dietary ecology of the parrots of southeastern Peru (Chapter 5) and that for some species a substantial portion of the population feeds on a daily basis (Chapter 3). However, river ways are important access routes in the Amazon where road infrastructure is still limited

(Killeen, 2007). Parrot claylicks will thus experience varying volumes of boat traffic, and in some areas local people hunt macaws at claylicks (Hammer and Tatum-Hume, 2003).

Claylicks have varying degrees of protection depending on their location: firstly by distance from centres of human settlement (Peres and Lake, 2003); and secondly by where claylicks are situated in terms of land use and management practises. In Peru, the best protected areas are the system of national parks, where human activity is restricted. Limited extractive land use is allowed in national reserves, while buffer zones offer limited protected status but are zoned as areas to encourage perceived sustainable economic practises such as tourism.

The Madre de Dios department of southeastern Peru is one of the best protected areas of Amazon rainforest, with 60% of the area encompassed by reserves, national parks or buffer zones (Salmón et al., 2003). The remaining forests of the Madre de Dios department are divided into various concessions (large areas of land provisioned to small companies or individuals for the purpose of a specific land use, most notably mining, Brazil nut harvesting, timber extraction and ecotourism). People associated with these activities offer varying degrees of tolerance to wildlife conservation, with timber extractors presenting an almost year round hunting presence (Schulte-Herbruggen and Rossiter, 2003), Brazil nut harvesters a seasonal hunting presence (Mori, 1992), while self-sufficient miners tend to hunt less. Ecotourism, conservation and reforestation concessions are governed by guidelines which restrict hunting.

The tourism and hospitality industry in general contribute a significant percentage of developing country GDP - in 2000, 193 million tourists visited developing countries leaving revenues of US$ 145 billion in the process (WTO 2002). Macaws and parrots are a vitally important part of the tourism packages offered by ecotourism companies in southeastern Peru (Brightsmith et al., 2008, Rainforest Expeditions, 2010). Macaws and large colourful parrot species have been highlighted as ambassadors for broader rainforest conservation initiatives, especially where they are common, predictable and where they provide visually entertaining spectacles and photographic opportunities (such as at claylicks) (Munn, 1998). However, there is concern about the credibility of the ecotourism industry, as many companies that market ecotourism products fail to live up to the principles of ecotourism (López-Espinosa, 2002, Fennell and Weaver, 2005). Ecotourism companies may be intentionally or unintentionally harming the wildlife and wildlife spectacles upon which they depend by not understanding or respecting flight distances of the wildlife that their tourists are viewing.

Hiking, wildlife observation, and other non-consumptive outdoor recreation can have considerable influence on the behaviour and distribution of wild animals (Klein et al., 1996, Constantine et al., 2004, Finney et al., 2005, Bejder et al., 2006). The impacts of boat traffic on shoreline birds are fairly well documented (Vermeer, 1973, Galicia and Baldassarre, 1997, Burger, 1998, Bright et al., 2004). In general, mobile birds move away from areas of high boat activity, whereas nesting birds show behavioral, growth, or reproductive effects (Rodgers and Smith, 1995), with varying degrees of habituation (Burger 1998). Motorized canoes cause antipredatory responses from macaws and parrots which may cause some birds to leave the area of a claylick totally (Burger and Gochfeld, 2003). If changes in animal behaviour resulting from direct human disturbance negatively affect the persistence of a given species or population, then these behavioural changes may lead to reduced survival and reproduction (Griffin et al., 2007). The impacts of boats and tourists on parrots at claylicks have not been formally quantified.

### 6.2.1 Aims

Determine the value and conservation status of claylicks in southeastern Peru, highlighting the role of tourism as well as its impacts on bird behaviour through tourist visitation and associated boat traffic. In so doing I provide information for the ecotourism industry to minimise disturbance of parrots at claylicks. To achieve this aim I have the following objectives:

1. Assess the value of claylicks to the tourist industry in southeastern Peru

2. Determine the degree of protection afforded to claylicks in southeastern Peru

3. Determine the likely impacts of boat-based and on-foot visitors to claylicks on parrot behaviour and daily feeding

4. Discuss the results of 1-3 in terms of the future of conservation strategies and ecotourism best practice for claylick visits

## 6.3 METHODS

### 6.3.1 Study sites

The study area in southeastern Peru has been described in Chapters 3 and 4. The impacts of boats and tourism at claylicks were examined at the Tambopata River claylicks Hermosa, Gato and TRC (Figure 6.1). Hermosa was located on the 250 m wide Tambopata River in the buffer zone of the Tambopata National Reserve and is associated with high boat traffic. This was the first claylick on the Tambopata River after an embarkation port and so all boat traffic associated with tourist lodges (up to 50 boats a day) had to pass this claylick.

### 6.3.2 Claylick economic value

Managers or owners of tourism enterprises operating in the Manu / Tambopata region were asked five simple questions/statements related to claylick value: rate the importance of claylicks in your marketing operations (from 1 low to 5 high); rate visitor satisfaction with claylick visits; how much would you pay for a claylick (in $US); how much would you charge other operators or tourists for entrance?; and do macaw claylicks deserved special protected status from the Peruvian government?

### 6.3.3 Spatial distribution of claylicks in relation to land use

A total of 62 parrot claylick locations were identified through systematic observations of five major rivers in the lowland Amazon of southeastern Peru (Chapter 3). Locations were plotted using ArcGIS 9.2 (ESRI). A 2006 database of protected areas, concessions, settlements and other land-use types for southeastern Peru was obtained from the Peruvian Institute for Natural Resources (INRENA). The number of claylicks occurring in each land-use type was calculated using HawthsTools ‘point in polygon’ tool (Beyer, 2004). A 10 km buffer zone of a database of settler communities was calculated using the Buffer feature (ArcToolbox) and merged in order to calculate the total area using the add AREA/PERIMETER to table tool in HawthsTools. The 10 km radius was used because this is the distance hunters in the Amazon basin are prepared to travel on hunting trips (Peres and Lake, 2003, Naughton-Treves, 2002).

### 6.3.4 Human impact on parrot claylick activity from boats and tourists

Monitoring of claylick use by parrots, boat traffic and tourist groups was conducted at the Hermosa claylick from January 2006 to December 2009 and at Gato and TRC data on claylick use by parrots and tourist groups were collected from January 2008 to December 2009. Gato was off the main river and received on-foot visitors only. Passing boat traffic was negligible at TRC since no lodges existed past the claylick there.

To monitor bird activity, observers arrived before daybreak in order to not disturb bird activity. The number of birds were recorded on the claylick every five minutes to quantify daily feeding activity (Brightsmith, 2004). An estimation of the total number of birds for each species was estimated (maximum count). A measure of seasonal variation was calculated from the daily feeding by dividing the three months with lowest feeding by the three months with highest feeding.

If birds flew from the trees or the claylick together in a large group, this was recorded as a flush (also known as an anti-predatory response). Responses to sources of disturbance (boats, tourists, mammals, birds of prey, other e.g. falling rocks) were classified as follows: 0 – no reaction, 1 – increase in alarm calls, 2 – slow dispersal of birds from the vicinity of the claylick, 3 – minor flush (up to 75% of birds take flight, but remain in the area), 4 – major flush (up to 100% of the birds take flight, but remain in the area), 5 – complete flush (100% of the birds take flight and leave the area completely for a time period of at least ten minutes). Responses were recorded separately for birds in the trees and on the clay. The time of all boats passing in front of the claylick were recorded, as well as direction of travel (upstream or downstream), engine type (peke-peke - a long-shaft ± 16 hp 2-cycle motor, or outboard motor – short propeller-shaft, quieter, 25 hp upwards) and how birds on the claylick or in the trees above the claylick reacted to the boat (using the flush categories described above). The closest distance to the claylick of each boat was recorded into five 50 metre bands, with 1 being close to the claylick at 0 – 50 m and 5 being furthest away at 200 – 250m.

The time of arrival and numbers of tourists visiting three claylicks (Hermosa, Gato and TRC) were recorded. Flush categories were applied to parrot responses to arriving tourists as described for boats above. The use of blinds (observation hides) was noted. Three observation points at TRC were located at different sections of the claylick (left, middle and right), at distances of 105, 150 and 80m respectively. Guides took their guests to where feeding activity had been observed most frequently. In order to determine the impact of tourist presence in relation to distance, the daily proportion of the total feeding was calculated for each of the three sections (left, middle, right) for each species of parrot.

### 6.3.5 Statistics

Data were tested for normality using histograms and appropriate parametric and non-parametric tests used as applicable. A one-way analysis of variance (ANOVA) was used to test the influence of distance of boats from the claylick on bird reaction. For this analysis boat distance was measured using the distance bands discussed above and bird reaction was the mean bird reaction. Mann-Whitney U tests were used to compare feeding at the claylick for each species with and without tourists, and overall differences in seasonality between claylicks for the parrot assemblage. Chi-squared tests were used to test seasonal variation in feeding at the claylicks between TRC and Hermosa for each species. Kruskal-Wallis tests were used to compare feeding pattern differences among claylicks and differences in boat traffic among months. Spearman’s ranked correlations were used to test the relationship between daily feeding patterns and tourist numbers.

## 6.4 RESULTS

### 6.4.1 Claylick value

Responses to the survey were received from eight ecotourism companies (Table 6.1; see acknowledgements for details). Respondents were unanimous in their belief that macaw claylicks should have some degree of official state protected status. All respondents would be willing to pay for a claylick, with responses ranging from US $4,000 to $100,000. Claylicks have an earning potential (according to how much these tour operators would charge other agencies) of up to $50 per visitor. With tourist numbers to Tambopata and Manu around 45,000 in 2005 (Kirkby et al., in press), claylicks have a potential maximum earning potential of $2,250,000 per year. A more realistic charge would be closer to $25 (Table 6.1), valuing claylicks at $1.08 million. Respondents pointed out that claylick value and charge rate would depend on the quality of the claylick in terms of numbers of birds and species.

Table 6.1: Value of claylicks in southeastern Peru from surveys of tourism operators from the Manu and Tambopata regions of southeastern Peru, n = 8 respondents.

| Metric | Mean ± s.d |
|---|---|
| Value of claylicks to tourism company marketing (1 low, 5 high) | 3.6 ± 0.9 |
| Satisfaction of claylicks as an ecotourism attraction (1 low, 5 high) | 3.9 ± 1.0 |
| Hypothetical single value payments for claylicks (x US$ 1,000) | 45.6 ± 40 |
| Hypothetical tourist access charge rates (US$) | 28 ± 16 |

### 6.4.2 Spatial analysis of claylicks and their protected status

Only 21 of 62 claylicks (34%) occur within state protected areas including buffer zones (Figure 6.1; Table 6.2). Since 16 of the 21 claylicks in state protected areas fall within buffer zones, where no conservation measures are enforced, only five claylicks (8%) are protected by reserves and national parks. Sixteen claylicks occur in private ecotourism or conservation concessions indicating that 60% of the claylicks mapped here (by no means a complete list of all the claylicks of Madre de Dios), are offered a degree of formal protection.

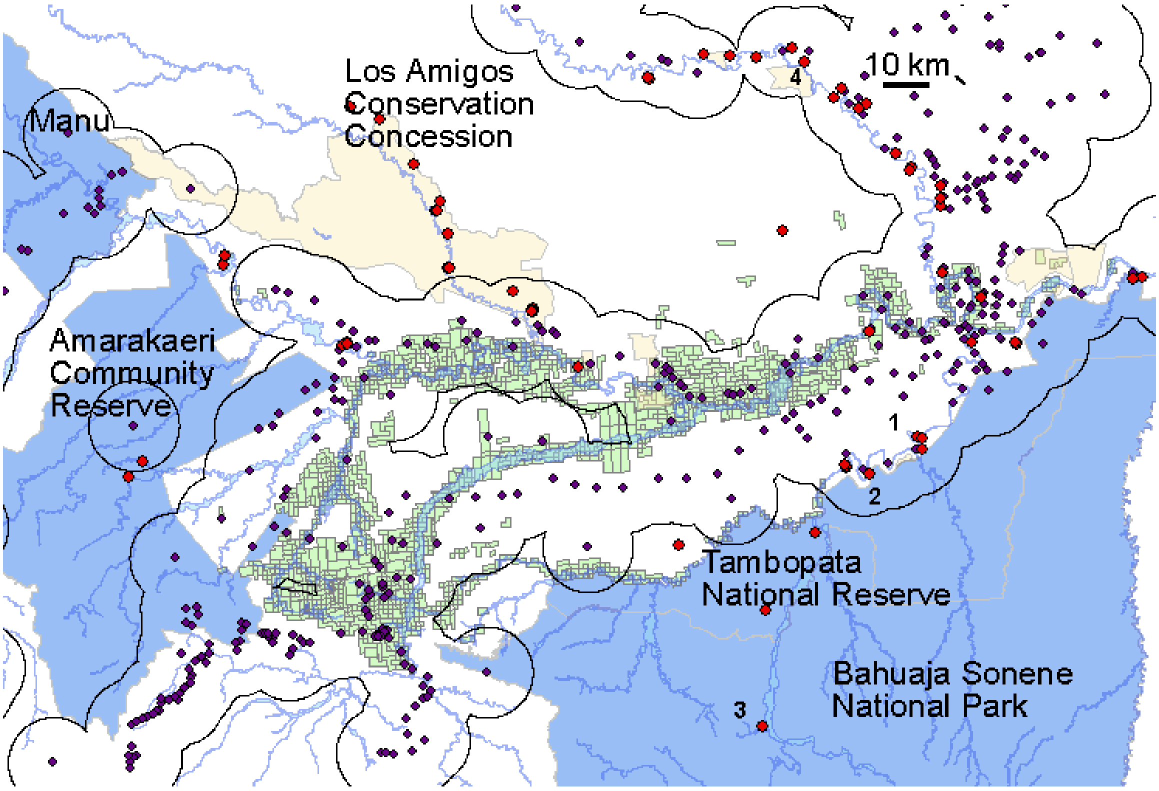

Figure 6.1: The location of 62 parrot claylicks (red circles) in southeastern Peru in relation to state reserves and national parks (blue), ecotourism or conservation concessions (pink) and mining concessions (green). The remaining areas are predominantly timber extraction and Brazil nut concessions, and private land usually used for small scale agriculture. Purple circles indicate community centres and the thin black line indicates a 10 km buffer (a zone within which hunting could reasonably be expected to occur). Monitored claylick locations: 1 – Hermosa, 2 – Gato, 3 – TRC.

A 10 km buffer zone of settlements in the study area was 27,337 km$^2$. Forty five claylicks (73%) occurred within the buffer. Twelve claylicks (19%) were located in INRENA's 'crisis zone' (an area of the Tambopata National Reserve and buffer zone deemed to be at high risk from illegal settlement, timber extraction and mining activities) at a density of 0.5 claylicks per 100 km$^2$.

Table 6.2: Claylick density (claylicks / 100 km$^2$) in southeastern Peru in relation to differing land use status.

| Land use | Total claylicks | Area (km$^2$) | Claylicks / 100 km$^2$ |
|---|---|---|---|
| *State protected areas* | | | |
| Bahuaja-Sonene National Park | 1 | 10,921 | 0.9 |
| Tambopata National Reserve | 2 | 2,783 | 7.2 |
| Tambopata Buffer Zone | 9 | 4,494 | 20 |
| Amarakaeri Reserve | 2 | 402 | 49.7 |
| Amarakaeri Buffer Zone | 7 | 716 | 97.8 |
| *Total state protected areas* | *21* | *19,317* | *10.9* |
| Brazil nut concessions | 0 | 726 | 0.0 |
| Ecotourism & conservation concessions | 16 | 2,222 | 72.0 |
| Native community | 3 | 204 | 146.7 |
| Titled lands | 4 | 3,433 | 11.7 |
| Wood extraction concessions | 1 | 1,018 | 9.8 |
| Mining concessions | 5 | 3,332 | 15.0 |
| Outside concessions and designated areas | 12 | | |

The highest claylick density occurred in land managed by native communities, although this was also the smallest total land use. Although the largest numbers of claylicks were located in ecotourism and conservation concessions, 14 (88%) were located in a single conservation concession of 1,466 km$^2$ while mean ecotourism concession size was 27.6 ± 26.3 km$^2$ (n = 24).

### 6.4.3 Ecotourism based threats to claylicks

On average 27 ± 8 boats pass Hermosa claylick between sunrise and 17h00 (n = 419 days). Boats with outboard motors (mostly used by tourist lodges) formed the majority of traffic while boats driven by peke-peke motors (used by local residents along the river) were less frequent (mean outboard: 17 ± 6 per day; peke-peke: 10 ± 4; t = 20.1, $p < 0.001$, df = 772). Tourist traffic typically travelled downriver in the early morning to take tourists to the airport, and back upriver in the afternoon with recently arriving tourists, resulting in a bimodal daily peak in boats passing the claylick per hour (Figure 6.2).

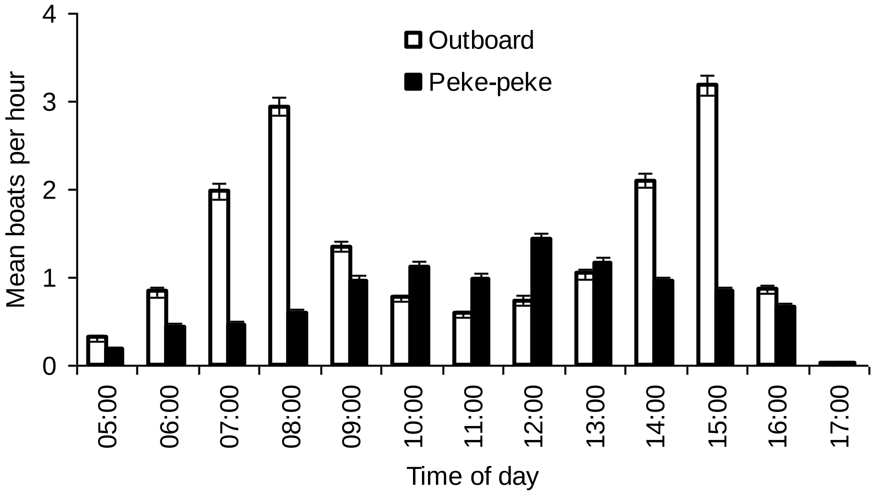

Figure 6.2: Hourly trends in boat traffic (mean boats per hour, error bars represent s.e.) for boats with outboard motors (associated with tourist movements) and peke-peke motors passing the Hermosa claylick from January 2006 to December 2009.

Peke-peke boats travelled further away from the claylick compared to outboard boats (outboards median zone, interquartile range: 3, 2 - 4; peke-peke: 4, 3 - 5; Mann-Whitney U test: Z = -29.9, $p < 0.01$). There was no significant difference between flush rankings for the two types of boats for parrots in the trees (outboard median flush ranking, interquartile range: 0, 0 - 1; peke-peke: 0, 0 - 1; Z = -1.6, $p = 0.11$), or birds on the claylick (outboard: 0, 0 - 1; peke-peke: 0, 0 - 1; Z = -0.3, $p = 0.81$). Compared to any other distance band, boats travelling within 50 m of the claylick caused significantly more flushes for both birds in the trees (one-way ANOVA; $F_2 = 25.5$, $p < 0.001$; Tukey HSD) and birds on the claylick (one-way ANOVA; $F_2 = 14.1$, $p < 0.001$; Tuskey HSD). Zones 3, 4 and 5, equivalent to beyond 100 m, formed a homogenous subset with lower rates of flushing. Beyond 100 m peke-pekes were more likely to cause a flush of birds from the trees than outboard motors (flush response for peke-pekes: 0, 0 - 2, outboard: 0, 0 - 1; Z = -2.5, $p = 0.01$), and this response was a trend for birds on the claylick (peke-peke: 0, 0 - 1, outboard: 0, 0 - 1; Z = -1.7, $p = 0.08$).

Tourist related boat traffic was seasonal, with more boats associated with tourist high season from April to November, peaking in August (Figure 6.3; Kruskal Wallis test $\chi^2 = 214$, $p < 0.001$, df = 11). At the monthly level, feeding for 5 of 6 early morning species was positively correlated with early morning outboard motor traffic (Blue-headed Parrot: $r_s = 0.67$, $p = 0.02$, n = 12; Chestnut-fronted Macaw: $r_s = 0.8$, $p = 0.002$, n = 12; Mealy Parrot: $r_s = 0.6$, $p = 0.04$, n = 12; Orange-cheeked Parrot: $r_s = 0.7$, $p = 0.02$, n = 12; Yellow-crowned Parrot: $r_s = 0.6$, $p = 0.03$, n = 12). Since the need for claylick use is independent of tourism and instead a regional phenomenon as seasonal patterns at claylicks away from boat traffic are generally correlated (Chapter 3), this suggests boat traffic does not negate natural seasonal patterns. However, the degree of seasonality (3 months with lowest feeding / 3 months with highest feeding) may be impacted as seasonal variation for parrot claylick activity for the parrot assemblage at Hermosa (with boat traffic) tended to be lower than at TRC (no boat traffic) (seasonality Hermosa median, interquartile range: 0.23, 0.15 – 0.27; TRC: 0.09, 0.07 – 0.11; U = 11, Z = -1.6, $p = 0.1$). The degree of seasonality between Hermosa and TRC was significantly different for Blue-headed Parrot *P. menstruus* ($\chi^2_1 = 8.1$, $p = 0.005$), Dusky-headed Parakeet *A. weddellii* ($\chi^2_1 = 15.1$, p < 0.001) and Cobalt-winged Parakeet *B. cyanoptera* ($\chi^2_1 = 24$, p < 0.001). However, the following species which also peak in feeding activity during tourist high season showed no difference in seasonal variation between sites: *A. severus* ($\chi^2_1 = 3$, $p = 0.08$) and Orange-cheeked Parrot *P. barrabandi* ($\chi^2_1 = 0.7$, $p = 1$), while Yellow-crowned Parrot *A. ochrocephala* showed greater seasonality at Hermosa compared to TRC ($\chi^2_1 = 7$, $p = 0.01$).

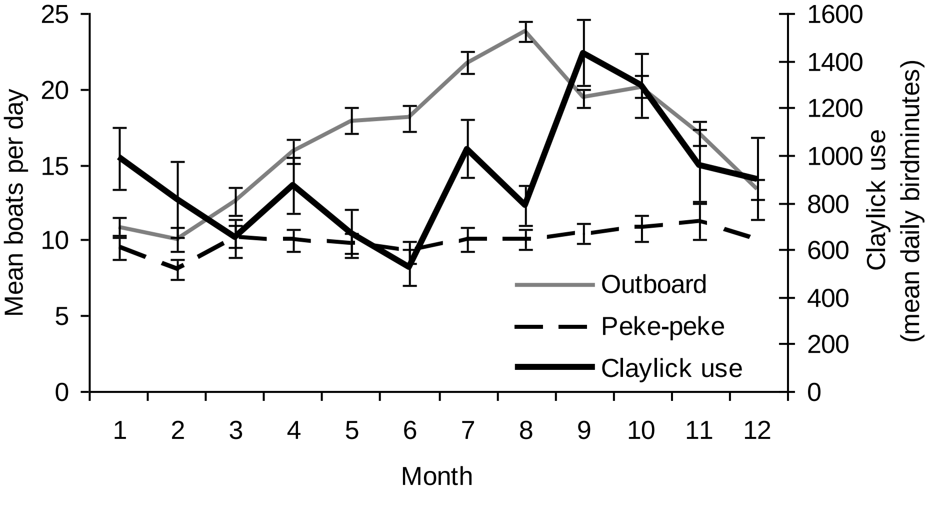

Figure 6.3: Annual patterns of boat traffic (outboard driven boats and peke-peke driven boats) and claylick use by all parrots at Colpa Hermosa, for the period 2006-2009. Bars represent standard error.

Tourists were present on 78.4% of days at Colpa Hermosa (n = 356). For days when tourists visited the blind, mean number of tourists visiting Colpa Hermosa per day before 08h00 was 8.01 ± 5.83 (n = 201), while the number of tourists visiting after 08h00 was 12.88 ± 9.48 (n = 241). At El Gato claylick, tourists were present on 55.7% of days, with group size 3.7 ± 5.9 (n = 130). There was no difference in early morning feeding between days with tourists present and tourists absent at either Gato (median, interquartile range for tourists present: 115, 0 – 460; absent: 15, 0 – 270; Z = -0.22, *p* = 0.83) or Hermosa (tourists present: 757, 325 – 1356; absent: 677, 281 – 1191; Z = -0.7, *p* = 0.5).

The capacity of the blind at Colpa Hermosa was 15 people. More than 15 tourists visited Colpa Hermosa on less than 9% of recorded early mornings. Three of the six regular early morning feeders fed in lower numbers when more than 15 tourists were present (Appendix 6.1: Blue-headed Parrot *P. menstruus,* Orange-cheeked Parrot *P. barrabandi* and Yellow-crowned Parrot *A. ochrocephala*). On 29% of days more than 15 visitors visited the claylick after 08h00. There was no difference between days when capacity was exceeded and days with fewer visitors for the four species that feed during this time (Appendix 6.1).

Tourists at TRC visited on 84.6% days and mean group size was 10.2 ± 8.3 (n = 416 days). Tourists generally arrived early (before 05h30) and never later than 08h00 and were seated on folding chairs with little or no concealment from the claylick. The following species fed less with tourists present: Blue-headed Macaw *P. couloni* (present: 10 ± 27, absent: 17 ± 38; Z = -2.1, *p* = 0.04) and Chestnut-fronted Macaw *A. severus* (present: 225 ± 381, absent: 369 ± 417; Z = -3.2, *p* = 0.002). Chestnut-fronted Macaw *A. severus* and Mealy Parrot *A. farinosa* showed significant negative correlations between daily feeding at the claylick and higher numbers of tourists (Appendix 6.2).

Eight species (57 %) fed in lower numbers in the presence of higher numbers of tourists at the extreme ends of the lick, associated with viewing sites closest to the claylick (Table 6.3). No species feeding at the middle section where the viewing area was located furthest away (and with traditionally the most amount of visitors) were impacted by higher tourist group size.

Table 6.3: Impact of tourist number on parrot feeding at different sections of the claylick at TRC. Correlations were conducted between tourist numbers and the proportion of the total amount of feeding that was observed at each section. Left, middle and right sides were 100, 150 and 80m respectively. Values for p where correlation is significant at the 0.05 level (2-tailed) are indicated in bold. n = 416.

| | Left side of lick | | Middle | | Right side | |
|---|---|---|---|---|---|---|
| | $r_s$ | *P* | $r_s$ | *p* | $r_s$ | *p* |
| All <08h00 species | -0.12 | **0.015** | -0.01 | 0.835 | -0.15 | **0.003** |
| Red-and-green Macaw | -0.01 | 0.912 | -0.02 | 0.716 | -0.06 | 0.259 |
| Blue-and-yellow Macaw | -0.02 | 0.701 | 0.02 | 0.71 | -0.11 | **0.027** |
| Scarlet Macaw | -0.05 | 0.269 | -0.03 | 0.589 | -0.10 | **0.039** |
| Blue-headed Macaw | -0.09 | 0.072 | 0.05 | 0.345 | -0.01 | 0.867 |
| Chestnut-fronted Macaw | -0.12 | **0.017** | 0.02 | 0.648 | -0.14 | **0.005** |
| Red-bellied Macaw | -0.12 | **0.017** | 0.00 | 0.963 | -0.14 | **0.005** |
| Mealy Parrot | -0.06 | 0.259 | 0.05 | 0.323 | -0.11 | **0.021** |
| Yellow-crowned Parrot | -0.11 | **0.024** | 0.07 | 0.151 | -0.11 | **0.024** |
| White-bellied Parrot | -0.14 | **0.004** | 0.08 | 0.101 | -0.05 | 0.36 |
| Blue-headed Parrot | 0.00 | 0.988 | 0.03 | 0.492 | -0.15 | **0.002** |
| Orange-cheeked Parrot | -0.135 | **0.006** | -0.01 | 0.836 | -0.083 | 0.091 |
| Dusky-headed Parakeet | -0.054 | 0.274 | 0.05 | 0.336 | -0.042 | 0.392 |
| White-eyed Parakeet | -0.206 | **0.01** | 0.09 | 0.068 | -0.05 | 0.305 |

## 6.5 DISCUSSION

### 6.5.1 The contribution of claylicks to the tourist industry in southeastern Peru

Tourist enterprises that have access to claylicks (which includes most of the Tambopata and Manu area operators) rank them very highly in terms of both their marketing and the satisfaction that they provide tourists. Although this study was not able to separate the value of claylicks from other ecotourism activities offered, such as boat trips, jungle walk, lake excursions and canopy towers, claylicks command a high price in the industry and furthermore have the potential to earn substantial amounts in tourist revenue. Munn (1992) calculated from revenues of Peruvian forest lodges and interviews with tourists that each large macaw could generate between US$750 and $4,700 in tourist receipts a year. The Hermosa claylick, where the maximum number of individuals observed around the claylick rarely exceeded 40 (Chapter 3), was considered a small claylick for the region and would value the claylick at $188,000 at

Munn’s (1992) upper value. This would make claylicks such as the one at TRC (valued in this study at $100,000) a good investment since the minimum number of macaws observed on a daily basis during the high season during 2009 exceeded 150 i.e. with the potential to earn $705,000 in tourist receipts. This natural capital has yet to be fully realized – a study of the value of claylicks as an attraction at one lodge showed that 60% of visitors had not even heard of claylicks, although the majority rated a visit to a claylick as one of their top attractions (Rensing and Zwerver, 2008). It also makes current national reserve entrance fees extraordinarily good value for money for tourists at the current time, with a one week permit $50 during 2009. As colourful birds, claylick photos and the experience tend to feature high on ecotourism marketing. However, tourism satisfaction was rated as mixed. This was probably due to the seasonal patterns associated with the claylicks and lack of activity associated with rainy weather. This needs to be considered if tourists are to remain satisfied with the expenses they are occurring.

### 6.5.2 The protected status of claylicks

Claylicks are often used as sites at which to conduct sit and wait hunting tactics (Montenegro, 2004). Large macaw claylicks probably have a catchment area of hundreds of square kilometres, as do the tapir claylicks of the region – with individuals travelling 10km or more in order to visit claylicks (Tobler, 2008). That a large proportion of the region’s parrot claylicks fall within the area for which it has been shown hunting has an impact (Peres and Lake, 2003) and that remaining macaw claylicks would all be accessible by boat is cause for concern. Although a large proportion of the region’s claylicks are afforded some degree of protection, either in national parks or ecotourism concessions, it has been recognised that there are limited resources within the existing natural areas management structure in order to ensure these sites will remain undisturbed and maintain their inherent value (Oliveira et al., 2007).

### 6.5.3 The impacts of visitors to claylicks on parrot behaviour and daily feeding

Ecotourism has the threefold goal of generating income from nature-based attractions, channeling support to protected areas and local communities, and creating rewarding, educational experiences for tourists (Kruger, 2005). Claylicks offer ideal natural capital for ecotourism and can in turn be better protected through ecotourism enterprise stakeholder participation – currently considered the best way of conserving Amazon rainforests and their resources (Campos and Nepstad, 2006, Christian et al., 1996). However, parties interested in pursuing concessions around claylicks need to be aware of the impacts that tourism in turn can have on the resource from which they aim to earn an income.

Birds can habituate to the presence of boats, but boats coming too close (<100m) to a claylick often cause anti-predatory responses. Boats may cause diurnal shifts in feeding behaviour. Chapter 3 shows diurnal patterns for three claylicks for large macaws, each displaying differing peaks in use. At Piedras and Gato, claylick use in tourist and boat low areas peaks in the mid morning. Although there is no boat traffic at TRC, here instead use of a trail system above the claylick during mid-morning periods may be pushing the feeding time to later in the day. At Hermosa, with combined boat and tourist traffic, there was no peak in feeding, with feeding observed throughout the day and into the mid-afternoon. Macaws may also feed for less time when faced with large amounts of boat traffic (Lee, 2006). Although our observations are from relatively few claylicks, the need for a cautionary management approach is recommended.

The true cost of disturbance may be underestimated in species that manifest few overt responses to human disturbance. Species with limited ability to move away from disturbance could suffer a high demographic cost (Gill et al., 2001). Impacts may also depend on age, for instance adult Hoatzins *Opisthocomus hoatzin* habituate to regular tourism but juvenile birds exhibit increased hormonal stress responses, reduced body mass, and lower survival than those at undisturbed sites (Müllner et al., 2004). Other apparently habituated animals display altered hormonal and behavioral responses to threatening situations e.g. habituated but highly disturbed Magellanic Penguins *Spheniscus magellanicus* have a reduced capacity to secrete corticosterone (Walker et al., 2006). Even where habituation does not result in physiological or behavioural changes, tolerance is unlikely to be absolute as animals continue to flee from some tourists and expend time and energy monitoring those outside the flight zone (Frid and Dill, 2002).

The fact that macaws seem to have habituated at the site showing greatest boat traffic may not necessarily mean that there has been no impact, as individuals that were sensitive to boat disturbance may have left the region before our study began (Bejder et al., 2006). This highlights the need to monitor relatively undisturbed claylicks in areas that face potential increasing boat traffic.

### 6.5.4 The future of conservation strategies and ecotourism best practise for claylick visits

Claylicks have no gazetted protected status under Peruvian law. These sites are a natural asset and should be a source of pride as no where else are claylicks as abundant or visited by as many individuals and species of birds (Chapter 2). The high value placed on claylicks by tourism operators in the region coupled with the large number of claylicks falling outside protected areas emphasizes how encouraging ecotourism concessions around claylicks is a logical way to extend protections to these natural assets using current land-management regulations, even if official state protection of claylicks is a long way off. If birds stop visiting claylicks or are reduced to below critical numbers where they no longer feel safe to feed, this will have severe consequences for the tourism industry.

It appears that birds can become habituated to the presence of boats, although boats approaching the claylick to within 100m are still a cause of concern. On narrower river systems, especially those with hunting, any boat traffic is liable to cause antipredatory responses (Lee, 2006). Human presence can impact feeding at claylicks negatively, and claylick observation protocols which reduce this impact need to be developed and adhered to in order to minimise the impact on birds. By doing so will improve the overall ecotourism experience. Over time tourism activities at some locations may compromise parrot physiology in a manner that limits conservation goals for the species and hence tourism.

Practical guidelines for tour operators that are based on parrot activity patterns may ensure more sustainable parrot-watching tourism. I advocate the use of blinds and would discourage groups without blinds to observe claylicks from a distance of less than 100 metres. However, as the visual impact of the birds can only be appreciated with a telescope beyond these distances, blinds with concealed approaches are recommended. These can be placed as close as 30 m from a claylick, as long as they are adequately constructed, tourist movement is restricted and access to the blinds are concealed. In Peru, all tourist groups visiting claylicks in protected areas do so with the company of a guide, as this is part of the park regulation system. This offers an opportunity to implement codes of best practise by introducing tourist group conduct concepts into the guide training curriculum. Ultimately, responsible tourism around claylicks will require a strong, well-enforced management plan and continued education of locals, tourists, and the tourist industry.

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Appendix 6.1: Impact of large tourist groups (>15 people) on claylick use at Hermosa: Daily claylick use (median birdminutes, interquartile range) for ten species of parrot, with Mann-Whitney U results. Results significant at the $p < 0.05$ level are presented in bold.

| | More than 15 tourists | 15 or fewer tourists | | | |
|---|---|---|---|---|---|
| Pre 08h00 species: | N=30 | N=326 | U | Z | *P* |
| *P. menstruus* | 0, 0 - 67.5 | 57.5, 0 - 143.75 | 3560 | -2.51 | **0.012** |
| *A. severus* | 0, 0 - 22.5 | 0, 0 - 40 | 4320 | -1.14 | 0.253 |
| *A. weddellii* | 5, 0 - 105 | 30, 0 - 258.75 | 4411 | -0.93 | 0.352 |
| *A. farinosa* | 0, 0 - 2.5 | 0, 0 - 15 | 4231 | -1.45 | 0.148 |
| *P. barrabandi* | 0, 0 - 0 | 0, 0 - 25 | 3888 | -2.13 | **0.034** |
| *A. leucophthalma* | 0, 0 - 0 | 0, 0 - 0 | 4770 | -0.87 | 0.386 |
| *A. ochrocephala* | 0, 0 - 77.5 | 27.5, 0 - 105 | 3560 | -2.53 | **0.012** |
| Post 08h00 species: | N=96 | N=260 | | | |
| *P. rupicola* | 20, 0 - 220 | 17.5, 0 - 191.25 | 12407 | -0.1 | 0.929 |
| *B. cyanoptera* | 0, 0 - 55 | 0, 0 - 5 | 11863 | -0.9 | 0.344 |
| *A. chloropterus* | 155, 50 - 345 | 170, 50 - 325 | 11952 | -0.6 | 0.54 |
| *A. macao* | 0, 0 - 0 | 0, 0 - 0 | 11963 | -1 | 0.312 |

Appendix 6.2: Tourist impact on parrot activity (Claylick use as median birdminutes, interquartile range) at TRC for 2008 and 2009, indicating differences between days with tourists present and absent, and correlations (Spearman’s) between feeding and total tourist numbers (n=415).

| | ABSENT | PRESENT | Mann-Whitney U | | | Correlations | |
|---|---|---|---|---|---|---|---|
| Species | Claylick use | Claylick use | U | Z | *p* | $r_s$ | *p* |
| *A. chloropterus* | 0, 0 – 0 | 0, 0 – 0 | 10851 | -0.5 | 0.644 | 0.04 | 0.395 |
| *A. ararauna* | 5, 0 - 105 | 25, 0 – 135 | 9839 | -1.5 | 0.144 | 0.08 | 0.094 |
| *A. macao* | 0, 0 – 15 | 0, 0 – 25 | 10096 | -1.2 | 0.22 | 0.02 | 0.719 |
| *P. couloni* | 0, 0 – 25 | 0, 0 – 10 | 9620 | -2.1 | **0.04** | -0.06 | 0.23 |
| *A. severus* | 265, 35 – 585 | 120, 15 - 270 | 8319 | -3.2 | **0.002** | -0.14 | **0.005** |
| *O. manilata* | 280, 15 – 780 | 182.5, 20 - 428.75 | 9459 | -1.9 | 0.062 | -0.09 | 0.069 |
| *A. farinosa* | 125, 0 – 1365 | 45, 0 - 617.5 | 9643 | -1.7 | 0.095 | -0.12 | **0.018** |
| *A. ochrocephala* | 20, 0 - 85 | 25, 0 - 108.75 | 10451 | -0.7 | 0.459 | 0.08 | 0.102 |
| *P. leucogaster* | 5, 0 – 85 | 27.5, 0 - 113.75 | 10079 | -1.2 | 0.234 | 0.03 | 0.546 |
| *P. menstruus* | 135, 5 – 350 | 80, 0 - 387.5 | 10864 | -0.3 | 0.797 | 0.03 | 0.53 |
| *P. barrabandi* | 25, 0 - 105 | 25, 0 - 133.75 | 11066 | 0.0 | 0.98 | 0.04 | 0.483 |
| *A. weddellii* | 110, 0 – 285 | 95, 0 - 260 | 10608 | -0.6 | 0.577 | -0.06 | 0.209 |
| *A. leucophthalmus* | 30, 0 - 370 | 35, 0 - 468.75 | 10950 | -0.2 | 0.871 | -0.03 | 0.614 |

# Chapter 7: Parrots and geophagy: an overview and future paths

## 7.1 The status of parrots in Peru

Although the parrot family is one of the most threatened large bird families in the world (Snyder et al., 2000, Bennett and Owens, 1997), it appears from this study that at least in the relatively intact and unfragmented Amazon rainforests of southeastern Peru populations are stable and mostly unthreatened. Of the 25 parrot species found in Madre de Dios (Chapter 1), only three are not classified as Least Concern (BirdLife International, 2009). However, trends in population growth for most of these species are unknown and consensus has yet to be reached on the status of some of these species. For instance Blue-headed Macaw *Primolius couloni*, classified as Least Concern in 2004 was then elevated to Near Threatened before jumping a rank to Endangered in 2006 (Tobias and Brightsmith, 2007). It has since been reclassified as Near Threatened in 2009 (BirdLife International, 2009), after a review of its status by Tobias and Brightsmith (2007). Density estimates produced in this study support this decision, as they fall within the predicted range. Although Tobias and Brightsmith (2007) also commented on the species association with successional forest, the macaw did not rank high on the index of successional forest preference produced in this account. Since I also show that successional forest species appear to use claylicks more, and the *P. couloni* is rare on claylicks over the region, I would reason that Blue-headed Macaw *P. couloni*, although found in successional forest, is not a successional forest specialist. I do not expect this species to become more common as increasing parts of its home range are converted to successional forest.

Instead, P. couloni distribution and abundance may be governed by environmental factors that determine the apparent species richness increase from southeastern to northwestern Madre de Dios. For instance, Amazonian Parrotlet *Nannopsittaca dachilleae* is classified as Near Threatened (BirdLife International, 2009) and not common on claylicks or transects along the Tambopata River, while incidental observations on claylicks along the Amigos and upper Madre de Dios Rivers show it is more common there. In fact, the species is a regular visitor to at least one claylick on the upper Madre de Dios River (*fide* Q. meyer). No research has targeted the status of this parrotlet – the only existing publication on this species is the original description (O'Neill et al., 1991).

Although hunting and pet trade were not a focus of this study, during the course of fieldwork very few direct threats such as hunting and extraction for the international pet trade market were observed, apart from small scale trade in parrots as pets in Puerto Maldonado. Indirect threats are of far greater concern. During a period of two weeks monitoring trees being brought into sawmills of Puerto Maldonado, around 500 trees were counted. Most (>50%) of these were large Ironwood *Dipteryx micrantha* - one of the primary nesting trees for macaws, parrots and other cavity nesters.

A history of woodcutting and wood extraction from the lower Tambopata River, where the Hermosa claylick is located, may explain the lower numbers of macaws visiting this claylick compared to other claylicks where macaws were observed. Numbers of macaws were stable over the four year period of this study, a possible indication that current conservation efforts after the declaration of the Tambopata-Candamo National Reserve and subsequent Bahuaja-Sonene National Park over the last decade have stabilised populations which still face harvesting for the pet trade, hunting and habitat loss outside protected areas (Herrera and Hennessey, 2007).

## 7.2 Parrot claylick distribution: global scale

The mapping exercise conducted during this study produced some surprising results and highlights the importance of a top down approach to many of the world’s interesting phenomena. That claylick abundance decreases from the western to the eastern parts of the Amazon, evidently correlating with an increasing environmental sodium gradient, allows one to examine predictions made for geophagy in other parts of the world. These patterns would be easy enough for researchers in Africa and Asia to map and examine using similar techniques, although even simple maps of occurrence and associated species richness would provide a visual overview of the scale of geophagy across other land masses. For instance, is the geophagy observed in African Gray Parrot *Psittacus erithacus* from the Democratic Republic of the Congo observed more than 200 km away from the coast, and if so, is there increasing use towards more central parts of Africa in the moist tropical zone? For Papua New Guinea (PNG), where some of the first records of parrot geophagy were published for southeastern Asia (Diamond et al., 1999), how does visitation rates of claylick species compare to parrot densities in the surrounding forests? Are similar proportions of the local populations visiting exposed soil?

From published accounts and the lack of a tourist industry focused on these sites, I would suspect that geophagy is nowhere near as predictable or as common as in the Amazon, simply as most of PNG falls within tropical storm deposition zones. No mention was made of geophagy in the many publications of the very species rich parrot communities of southeastern Asian and its islands (Anggraini et al., 2000, Marsden, 1998, Marsden and Pilgrim, 2003, Marsden et al., 2001, Cahill et al., 2006, Walker, 2007). Diamond (1999) mentions that 37 predominantly frugivorous birds (77%) observed in their study area in PNG did not consume soil. A more recent study in the Eastern Highlands of Papua New Guinea reported similar numbers (Symes et al., 2006). Counts of the total PNG assemblage reached ‘100 or more’ individuals, while on-clay counts at even the smallest Tambopata claylick for a single species would regularly reach 200 and up to 1,700 individuals of the local parrot assemblage have been counted at TRC (Brightsmith, 2006). I would predict that isolated sites (such as those in PNG where ‘geophagy sites are sparsely distributed and attract birds over a large area’ (Diamond et al., 1999)) would attract greater numbers of species and individuals based on species richness patterns for isolated claylicks as described in Chapter 3. That they do not do so indicates that the underlying drive that results in ‘craving’ (Vermeer and Farrell, 1985) for soil by parrots in PNG is mostly absent, and instead where craving for sodium is possibly observed this results in only small numbers of birds drinking from salty springs or consuming soil associated with these (Symes et al., 2006).

## 7.3 Reasons for parrot geophagy

Since the publication of the 1999 papers showing that claylick soils can bind dietary toxins (Gilardi et al., 1999, Diamond et al., 1999) consumption of soils by parrots to protect from dietary toxins is often the *de facto* reason given for avian geophagy (e.g. Symes and Marsden, 2003) and the importance of mineral supplementation is stated ‘an unlikely cause of geophagy in parrots, humans and nonhuman primates’ (Dominey et al., 2004). The Diamond et al. (1999) publication on geophagy was based on only two consumed soils samples and no control samples, based on Gilardi’s (1996) observation that soil analysis from sites are ‘virtually identical’. The later conclusion is flawed as most other subsequent analysis have shown that small differences in some macroelements e.g. sodium at specific sites, can explain preferences in bird use (Brightsmith and Aramburu Munoz-Najar, 2004, Brightsmith et al., 2008, Powell et al., 2009). This means the conclusions based on Diamond et al. (1999) results need to be treated cautiously – especially '… acquisition of essential minerals is unlikely to provide the explanation for the avian geophagy observed in New Guinea and Peru'. That negatively charged cation-exchange sites bind positively charged alkaloids (quinine and strychnine) and to a lesser extent tannic acids by no means invalidates minerals, especially sodium, from being the driving force resulting in hundreds of individuals from a range of bird species consuming clay on a daily basis across South America.

My study did not focus specifically on the reasons for geophagy, but a broad conclusion from both the use of claylicks across South America (Chapter 2), as well as the dietary components of this study (Chapter 5), lean towards regular parrot geophagy to be driven for nutrients, most likely sodium. Ultimately, soils are as diverse in their chemical and physical properties as the many rocks, geomorphological and environmental factors that create them. It is unlikely that there is a unifying theory for geophagy and instead soil will be consumed to satisfy the diverse dietary needs of animals when the properties of the soil in a location is discovered and the benefits thereof learnt across the local community.

## 7.4 Parrot claylick distribution and temporal patterns of use in southeastern Peru

All the parrots of the lowland forests of southeastern Peru can be viewed at one or other claylick and continue to provide a visual spectacle regularly billed as one of the most amazing natural wildlife phenomenon in the world. Southeastern Peru has the ideal combination of factors that create a claylick rich landscape: a large parrot community, sodium poor conditions, and nutrient rich clays which are being elevated and so are exposed during wet periods when parrot use them most (Chapter 2). However, the modelling exercise undertaken to understand the extent of geophagy across South America also showed that incidents of documented geophagy are underrepresented in the literature and that areas with limited access or research may have large claylicks as yet unreported.

Southeastern Peru has some of the highest claylick densities recorded. Claylicks of the Tambopata River have high visitation rates and high species richness perhaps both due to their wide spacing and the need of the parrot assemblage to use claylicks. Claylicks on the Piedras and Amigos rivers may be more dynamic as vegetation and erosion would change the sites where birds feed more regularly. Some sites recorded as claylicks previous to the claylick survey were found to be abandoned. Birds can be skittish and will feed less after an erosion event dramatically changes the appearance of the site they used to feed on (Hammer and Tatum-Hume, 2003). We also observed that their exploratory nature would mean that they would visit banks cleared of vegetation, even if they subsequently decided those sites were not as good as the ones they had preferred previously. Clearing of vegetation to open up favourable banks of soil has been observed to attract birds during previous studies (Burger and Gochfeld, 2003).

In the case of TRC when no trees suitable for perching were located near the claylick, the unique phenomenon of the ‘dance’ was observed – birds would fly back and forth for several minutes before descending. During 2009, while vegetation was growing up around the TRC claylick, whereas birds had fed mostly together previously there were subsequently clear sites preferred by different species which could possibly be better accounted for by claylick microdynamics e.g. exposed soil surface (macaws will prefer large exposed areas), texture (smaller species have been observed to feed on broken off sections of clay since the hard surface means biting off chunks poses problems even for small species), as well as local vegetation dynamics (parrot members that are green may prefer to sit in leafy bushes, or bushes species such as *Inga* in the case of White-bellied Parrot *P. leucogaster* as the dappled leaf texture enhance that species colouration and so is better for camouflage). Many of these anecdotal observations could be more rigorously explored in future studies.

Spatial and temporal patterns of claylick use were complicated by accessibility issues, the skittishness of the birds, and the long periods over which monitoring needs to be conducted to account for seasonal and disturbance related variables. Diurnal feeding patterns common to species at claylicks spread far apart suggests that predation mitigation strategies may be a factor. Seasonal patterns of claylick use that hold across the region are explained by the breeding season where adults feed clay to their chicks, as previously postulated by Brightsmith (2006, , 2010). Our understanding of daily fluctuations in bird numbers and the reasons therefore would be improved by a study that focuses on multiple, closely located claylicks for as many consecutive days as possible.

Based on density estimates (Chapter 4), it appears that only 1 – 10% of the local population of parrots feeds at the claylick on any given day. Only up to 10% of the local macaw population is expected to breed during any one year due to nest site scarcity (Nycander et al., 1995). If only 1% of the birds within 10 km radius use the claylick on a given day on during the low season, and then all breeders use the claylick during breeding, then that could cause the 5x to 10x increase in claylick use observed between seasons.

The role of cultural memes (e.g. Payne et al., 1988) which enable species to learn to use claylicks in different areas should be further explored to account for species present in the vicinity of certain claylicks, but which never showed interest in feeding there. The lack of a clear answer to why species that consume clay elsewhere avoid certain claylicks indicates that our understanding of parrot behaviour at and around claylicks is far from complete.

A more comprehensive mapping program of the parrot claylicks along all Madre de Dios river systems should be undertaken. Extending the themes developed here for the parrot family should be extended to the entire suite of animals that engage in geophagy – patterns for primates and other birds may well prove to be different, as possibly are the driving reasons behind their geophagy.

Although this small budget study has elucidated several aspects of parrot ecology, especially in their relation to claylick use, there are still many unanswered questions that would be better addressed through more expensive studies using telemetry studies across the parrot assemblage. These would allow better information on gender related visitation patterns, frequency of claylick use, and distances that birds are willing to travel in order to visit claylicks. What parrots in distant *tierra-firme* forest do to supplement sodium (or mitigate dietary toxins) remains unknown.

Southeastern Peru had the highest concentration of claylicks of any location across South America. For this reason alone the area should attract greater conservation efforts to stem the tides of destruction arising from mining, large-scale agriculture, colonisation and non-sustainable land use practises (Dourojeanni, 2006).

## 7.5 Parrot abundance

Few abundance estimates have been produced for parrots in tropical forests, or anywhere, due to the difficulties in detecting birds in the upper canopy and for meeting basic assumptions of Distance sampling (Rosenstock et al., 2002). Although Variable Circular Plots are often used to census birds, the number of points needed to produce density estimates for all but the most common species means few density estimates have emerged from general bird surveys (Marsden, 1999). Line transects are better suited to large, colourful species and maximise time spent in survey effort (Bibby et al., 1998, Buckland et al., 2001). Despite the applicability of Distance sampling to produce density estimates for most of the parrot family, an adequate means for determining small species (parrotlet) densities in tall canopy environments and rare species has yet to be found.

By accounting for changes in detectability through bird vocalization rates by species and season, I have introduced a simple method for addressing the violation of the key assumption of Distance sampling that all birds on the line of the transect are detected in forest environments (Buckland et al., 2008). A vocalisation study can be conducted at the same time as a bird survey and produce multipliers which will improve density estimates.

This study showed that floodplain forest had higher numbers of parrots than *tierra-firme* forests, but that there was also a large degree of variation for most species between dry and wet seasons. In southeastern Peru, part of this may be due to the presence of claylicks for some species, and sampling should not be conducted for species that use claylicks within 2 km of a claylick. However, parrot densities in southeastern Peru do not appear to be greater than those in other tropical environments, so despite the presence of claylicks the carrying capacity of the forests for the parrot family is not greater. Whether parrot abundance would be lower in the absence of claylicks would be difficult to test, but a comparison with the forests of northern Peru would be useful to compare sites with low sodium and generally similar overall other environmental factors.

The dietary analysis (Chapter 5) showed that density changes were correlated with the availability of plant species that were less common across the landscape. The tracking of resources across landscapes has been recorded for a wide spectrum of birds, including parrots (Renton, 2001) and may account for seasonal differences between forest types.

## 7.6 Parrot feeding ecology

The large parrot assemblage that exists in southeastern Peru does so through niche differentiation both through dietary breadth and dietary specialization. Sufficient ecological niches are made available by the high tree species richness combined with food availability on a year round basis.

This study did not focus on secondary or successional forests, but it appears that parrot species associated with these habitats tended to be highest claylick users. A future focus for claylick studies should be to differentiate whether the use of claylicks was higher for this group simply because of proximity to the resource, due to nutrient deficiencies, or because these species are faced with a suite of more toxic species. Since clays protect the gut against certain dietary toxins, perhaps the only conclusive way to show that the parrot community of southeastern Peru gains any benefit with regards protection from dietary toxins would be to compare longevity in this community of wild parrots with areas where clay consumption is not observed. This would be nearly impossible to do given that parrots are hard to catch, long-lived and finding any area that has stable populations free from anthropogenic disturbance over a long period would be almost impossible. It is thus likely that this polarising debate will continue for the foreseeable future, with both hypotheses for claylick use accumulating evidence for and against.

## 7.7 Guidelines for tourism at claylicks

The earning value of claylicks is very high, and their presence is rated highly by tourist operators in the southeastern Peru. Although a handful of claylicks are well protected by their location in and around protected areas, most are easily accessible to determined hunters. Ensuring the long term persistence of claylicks may require state intervention, but could be solved by encouraging ecotourism concessions around existing claylicks outside protected areas.

Boat traffic and tourist presence have an influence on parrot activity at claylicks, but these impacts can be mitigated by keeping appropriate distances and with the use of observation blinds. It was also apparent that many ecotourism enterprises were acting in ignorance as to the consequences of their actions around claylicks, and when approached certain operators where amenable to changes in boat operation procedures. However, guides of companies that are considered responsible would often arrive late at claylicks, and although we did not thoroughly document the impact of human movement on the birds, the impression was that this was a greater cause for disturbance compared to elevated noise levels. For claylicks with poor, i.e. unconcealed, access to blinds it should be clear that should visitors fail to be ready before activity begins, then the visit will no longer be possible.

Observation points (blinds) should be fixed at preferred feeding points, and access should be prohibited to alternative feeding sites that birds may flee to as a secondary choice when faced with human related disturbance. In order to encourage feeding at permanent sites, these can be managed by clearing encroaching vegetation and the placement or management of perch sites. Doing so allows the birds better access to preferred sites while enhancing the ecotourism experience.

With boat movements, especially around claylicks where boat traffic is low and birds are more liable to flush, movement should not be allowed within 100m of a claylick during periods of peak activity i.e. from 05h30 to 07h30 when most parrots and parakeets feed and from 09h00 to 12h00 when the larger macaws and some of the parakeets prefer to feed.

## 7.8 Conservation implications

Hunting of a wide range of animals at claylicks is registered for across the region (Montenegro, 2004, Tatum-Hume, 2006, Alexiades, 1999). Since both birds and mammals visit claylicks from large areas away and not on a daily basis, regular hunting could occur without a hunter noticing any apparent change in visitation rates but while depleting the surrounding forests from all claylick dependent species (Tobler et al., 2009). As such, it is the area’s best interests to implement state protection of claylicks as natural heritage sites. It would be beneficial to highlight the importance of these sites through the media, to generate general pride and conservation concern for one of the world’s most spectacular wildlife phenomena.

The use of claylicks is very likely a barometer for the health of the local populations of parrots and other animals that use them. Claylicks should continue to be the subject of ongoing long-term monitoring in order to understand the consequences of ongoing land-use change, and of both local and global environmental impacts. Ecotourism and conservation concessions offer a relatively uncomplicated means of extending protected status to the region's major claylicks. Potential tourism candidates should be thoroughly reviewed to ensure long-term commitment, environmental track record and financial security. A monopoly on access to claylicks should not be allowed.

This study has broadened our knowledge on the claylicks of South America and a community of parrots that use them. However, it has also shown that much has yet to be learnt about the parrots that use them and highlights the needs for further ecological studies. Long term monitoring projects currently in progress should be supported, as they will detect any critical changes in parrot density or human disturbance that will negatively impact a valuable phenomenon in both terms of economic value and ecological functioning.

## 7.9 References

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