The Psittacine Year:

What drives annual cycles in Tambopata's parrots?

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Introduction

Psittacines are notoriously difficult to study in the wild (Beissinger & Snyder 1992). Due to their lack of territorial behavior, vocalization behavior, long distance movements, and canopy dwelling nature, many general bird community studies do not adequately sample parrots (Casagrande & Beissinger 1997; Marsden 1999; Masello et al. 2006). As a result, detailed studies of entire parrot communities are rare (but see Marsden & Fielding 1999; Marsden et al. 2000; Roth 1984). However, natural history information is important for understanding and conserving this highly endangered family (Bennett & Owens 1997; Collar 1997; Masello & Quillfeldt 2002; Snyder et al. 2000).

The lowlands of the western Amazon basin harbor the most diverse avian communities in the world (Gentry 1988) with up to 20 species of macaws, parrots, parakeets, and parrotlets (Brightsmith 2004; Montambault 2002; Terborgh et al. 1984; Terborgh et al.

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1990). Psittacine densities can also be very high in this region as hundreds to thousands of parrots congregate daily at riverbanks to eat soil (Brightsmith 2004; Burger & Gochfeld 2003; Emmons 1984; Nycander et al. 1995). These "clay licks" apparently provide an important source of sodium and protect the birds from the toxins in their diets (Brightsmith 2004; Brightsmith & Aramburú 2004; Emmons & Stark 1979; Gilardi et al. 1999).

Parrots eat predominantly seeds, unripe fruit, ripe fruit, and flowers, supplemented occasionally with bark and other items (Forshaw 1989; Renton 2006). Unlike many other birds, New World parrots are apparently not able to switch to diets of predominantly insects and for this reason are intimately linked to the fruiting and flowering patterns of trees. While climate fluctuations in the tropics are notably less than in temperate zones, tree fruiting and flowering are known to vary seasonally in every location they have been studied (Adler & Kielpinski 2000; Croat 1975; Frankie et al. 1974; Lugo & Frangi 1993; van Schaik et al. 1993; Zhang & Wang 1995). Few plant species fruit and flower year round, meaning that different foods are available to parrots at different times of year. In addition total food abundance fluctuates in response to seasonal rainfall patterns (van Schaik et al. 1993). These annual variations in food supply have important implications for psittacine life history patterns. For example a lack of food can drive some or all members of a species to move to other areas, following available food resources (Powell et al. 1999; Renton 2001). Nesting season and nesting success can also be tied to annual fruiting and flowering patterns (Sanz & Rodríquez-Ferraro 2006).

To effectively conserve parrot populations in the modern landscape, we need detailed knowledge of their requirements and natural history cycles. Only in this way can we ensure that the correct habitat elements are protected at the correct spatial scale.

The current study uses data on parrot and macaw nesting (7 years), soil consumption (7 years), seasonal changes in abundance (3 years), and tree phenology (2 years) from Tambopata Research Center, Peru to analyze annual life history patterns and explore possible causative links among the different factors.

Methods

Study area

The study was conducted at Tambopata Research Center 13º 07′ S, 69º 36′ W. The center is on the border of the Tambopata National Reserve (275,000 ha) and the Bahuaja-Sonene National Park (537,000 ha) in the department of Madre de Dios in southeastern Peru. It lies at the boundary between tropical moist and subtropical wet forest at 250 m elevation and receives 3,200 mm of rain per year (Brightsmith 2004; Tosi 1960). The dry season extends from April – October during which monthly rainfall averages 90 to 250 mm (Brightsmith 2004). The research center is located in a small (<1 ha) clearing surrounded by mature floodplain forest, successional floodplain forest, *Mauritia flexuosa* (Arecaceae) palm swamp, and upland forest (Foster et al. 1994). A large patch of bamboo (*Guadua sarcocarpa:* Poaceae) covered the area immediately adjacent to the clay lick, but this patch flowered and died in 2001 to 2002 (Foster et al. 1994; Griscom & Ashton 2003). The clay lick is a 500-m long, 25 to 30-m high bank along the western edge of the

upper Tambopata River approximately 1 km from the research center. The cliff is formed by the Tambopata River's erosion of uplifted Tertiary age alluvial sediments (Foster et al. 1994; Räsänen & Linna 1995; Räsänen & Salo 1990). The soils of the lick are rich in clay with high cation exchange capacity and high sodium levels (Gilardi et al. 1999), DJB unpubl. data).

Tree phenology

Community wide tree phenology patterns have been monitored since July 2004 using monthly direct observation of 1650 trees spread among four habitats (*terra firme* forest, mature floodplain forest, succession river edge forest, and *Mauritia* palm swamp, K. Quinteros unpubl. data). We used these data to generate a rough index of potentially available psittacine food by calculating the proportion of trees that contained flowers, unripe fruits or ripe fruits, as all three are commonly consumed by parrots (Forshaw 1989). Data were collected in July and August of both 2004 and 2005. The data we present represent the average values for July and August. As we are still compiling the lists of species eaten by psittacines at the site and identifying the 1650 trees, the data presented here include all tree species not just those eaten by psittacines.

Parrot nesting

Researchers monitored Scarlet Macaw (*Ara macao*) and Red-and-green Macaw (*Ara chloropterus*) nests in nest boxes and natural tree cavities from November 1999 – April 2006. Nests were checked once every 1 to 7 days throughout the breeding season (November – April). Nests were climbed using single rope ascension techniques and chicks were weighed and measured on each climb (Nycander et al. 1995). Researchers

and guides working at the site have opportunistically recorded nests of other psittacine species since 1990. We only have detailed annual nesting chronology for Scarlet and Red-and-green Macaws. For most other species we have found only a few nests since 1990 (Brightsmith 2005). For this reason data from all years are pooled to provide a composite estimate of nesting season for each species. Lumping across species is justified based on the detailed data from Scarlet and Red-and-green Macaws which show little annual variation and great synchronization for these.

Parrot abundance

To determine the abundance of parrots in the forests around the study site, researchers conducted 10-minute point counts from January 2003 – December 2005. A total of about 900 point counts were completed per year at a total of 18 different points spread among four different habitats (terra firme forest, mature floodplain forest, succession river edge forest, and *Mauritia* palm swamp). Each point is separated by at least 400 m from every other point. Observers recorded all parrots seen or heard, the number in the group when seen, and the approximate distance to perched birds. The index of parrot abundance presented here is the monthly average number of groups (including flying and perched birds) recorded per 10-minute point count. Since clay lick activity is most intense in the morning, censuses were carried out in the afternoon (after 15:30) to avoid inflated encounter rates caused by birds flying to and from the clay lick (Brightsmith 2004).

Soil consumption

Observers recorded bird use of the clay lick during approximately 20 early mornings per month from February 2000 – December 2005. Researchers were at the site before the

birds began arriving (approximately at sunrise) and stayed until the birds finished their early morning lick use (usually before 07:30 EST). Every 5 min observers recorded the weather as rain (rain falling on the observer), sun (sun hitting the ground anywhere in the vicinity of the clay lick), or cloud (if neither of the others applied). The presence or absence of fog was also noted. 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 5 min using binoculars and a spotting scope (Brightsmith 2004). The index of clay lick use presented here is bird minutes. For example if 5 parrots spend 10 minutes on the clay lick this counts as 50 bird minutes. Bird minutes are used here instead of maximum number of individuals per species or other metrics because bird minutes is best thought to represent the total amount of clay consumed, and not just the number of birds in the area.

Data analysis

I tested the relationship between body size and the onset of breeding using a Spearman rank correlation of body mass versus month of first breeding and a *t*-test of month of first breeding for large (>250 g) versus small (<250 g) psittacids (Gibbons 1985). Spearman rank correlations were also used to test the relationships among 1) number of parrot species nesting per month and the percentage of trees with flowers or fruit, 2) the monthly average parrot abundance from the census data and the percentage of trees with flowers or fruit, and 3) the monthly average clay lick use and the parrot abundance from census data.

Results

A total of 21 parrot species in 14 genera have been recorded at Tambopata Research Center. Two species, Red-shouldered Macaw (*Diopsittaca nobilis*) and Red-crowned [Painted] Parakeet (*Pyrrhura [picta] rosifrons*), have never been recorded by myself or my research teams (Table 1). Two additional species, Tui Parakeet (*Brotogeris sanctithomae*) and Scarlet-shouldered Parrotlet (*Touit huetii*), have been recorded by the research teams only once and four times respectively. This leaves a total of 17 species that are seen annually at the site. As detailed articles of this information are being prepared for publication elsewhere, what follows is only a cursory analysis and discussion of these results.

Tree phenology

The percentage of trees with flowers, unripe fruits, or ripe fruits was lowest (< 10%) in the late wet season early dry season (February to May) and gradually increased to a high in the beginning of the wet season (November to January, ≥ 16%, Fig. 1).

Parrot nesting

I have nesting information for 15 of the 20 parrot species occurring at the site (Brightsmith 2005, Table 1). The parrot nesting season runs from June to March. Most parrots and parakeets bred from June to November, whereas the macaws, Mealy Parrot (*Amazona farinosa*), and White-eyed Parakeet (*Aratinga leucopthalmus*) nested from November to March. Smaller parrot species initiated nesting significantly earlier in the season than larger parrots. This trend held for all 15 species (rank correlation: $r = 0.70$; t-test: $t = 3.08$, $P = 0.009$; species listed in Table 1) and for the 11 species where I

observed chicks or eggs (rank correlation: $r = 0.81$; t-test: $t = 5.25$, $P <0.001$, Brightsmith 2005).
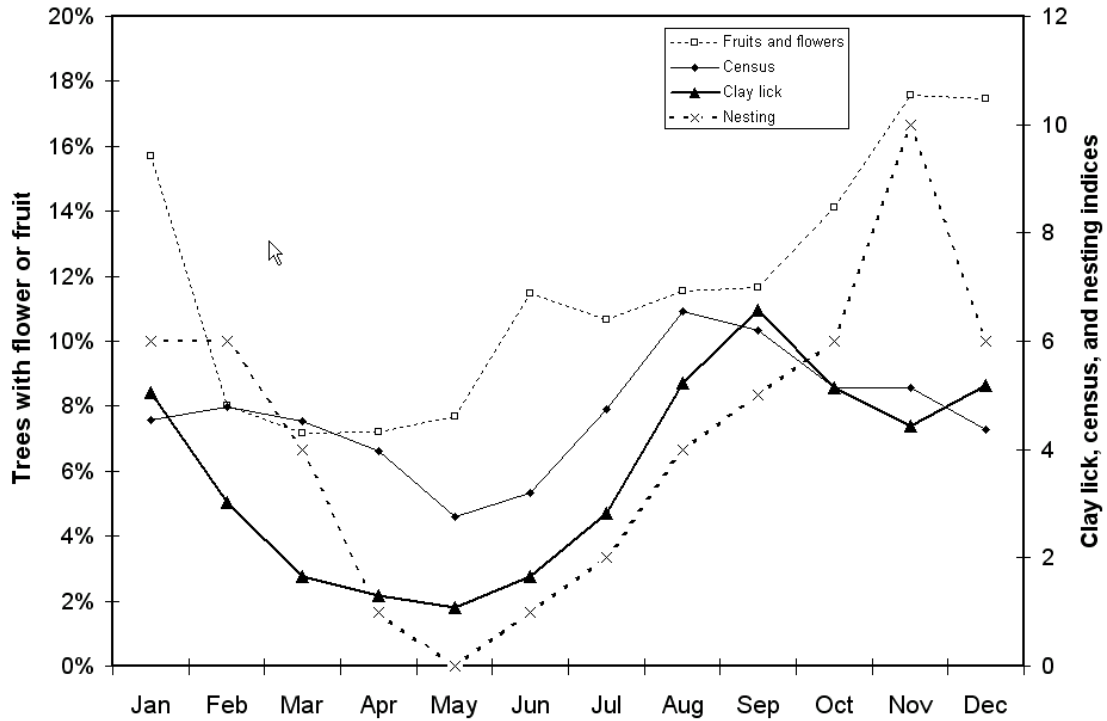

Figure 1: Annual patterns of tree phenology and parrot life history at Tambopata Research Center, Peru. Data for all variables are combined for all psittacine species and across all years of the study. Tree phenology is presented as the monthly percentage of trees with flowers or fruits. Censuses are the monthly average number of parrot groups encountered per 10-minute census. Clay lick data are monthly averages of lick use for all species combined presented in thousands of bird minutes (5 birds on the lick for 10 minutes = 50 bird minutes). Nesting is the number of parrot species known to nest in each given month (N = 11 species for which we have confirmed nesting season by seeing eggs or chicks).

Table 1: Psittacine species recorded at Tambopata Research Center. Body masses are from Dunning (1993). Start of nesting is from Brightsmith (2005) and unpublished data. Clay lick use abundances are given as common (seen during ≥75% of the daily observations), uncommon (seen < 75% and ≥ 25%), rare (seen < 25% and ≥5%), or occasional (seen during <5% of the observations, Brightsmith 2004). For censuses abundance is given as common (detected ≥ once per hour), uncommon (detected < once per hour and ≥ once per 2 hours), rare (< once per 2 hours and ≥ once per 10 hours), and occasional (< once per 10 hours). Latin names

Species	Mass (g)	Start of nesting	Clay lick	Census
Blue-and-yellow Macaw	1125	November	Common	Common
Scarlet Macaw	1015	November	Common	Common
Red-and-green Macaw	1250	November	Common	Common
Chestnut-fronted Macaw	430	November	Common	Common
Red-bellied Macaw	370	October	Common	Rare
Blue-headed Macaw	250	? [2]	Rare	Occasional
Red-shouldered Macaw [1]	136	?	Never	Never
White-eyed Parakeet	157	October ? [3, 4]	Uncommon	Uncommon
Dusky-headed Parakeet	108	? [2]	Uncommon	Common
Painted Parakeet [1]	65	September [4]	Never [5]	Never
Black-capped Parakeet	75	? [2]	Never [5]	Occasional
Cobalt-winged Parakeet	67	August [4]	Uncommon	Common
Tui Parakeet	59	August [4]	Occasional	Never
Dusky-billed Parrotlet	25	? [2]	Rare	Occasional
Amazonian Parrotlet	42	July ? [3]	Occasional	Never
Scarlet-shouldered Parrotlet	60	August ? [3]	Never	Never
White-beillied Parrot	155	September	Uncommon	Rare
Orange-cheeked Parrot	140	? [2]	Uncommon	Rare
Blue-headed Parrot	247	June	Common	Common
Yellow-crowned Parrot	510	July ?	Uncommon	Uncommon
Mealy Parrot	610	December	Common	Common

[1] Never seen at the site by the author, records from other observers
[2] Nesting season unknown
[3] Nesting season suspected through observations of birds at nests or interviews with reliable local people, however not confirmed by the author
[4] Nesting data from nearby Manu National Park
[5] These species have been seen consuming soil at other clay licks

Parrot abundance

A total of 3040, 10-minute point counts over 3 years produced broadly repeating annual patterns of parrot abundance at Tambopata Research Center. Abundance peaked in the late dry season (August to September) with 6 or more psittacine groups detected per 10-minute count in 2003 (Fig. 2). Each year the lows occurred in the early dry season (May to June) with about 3 groups registered per 10 minutes.
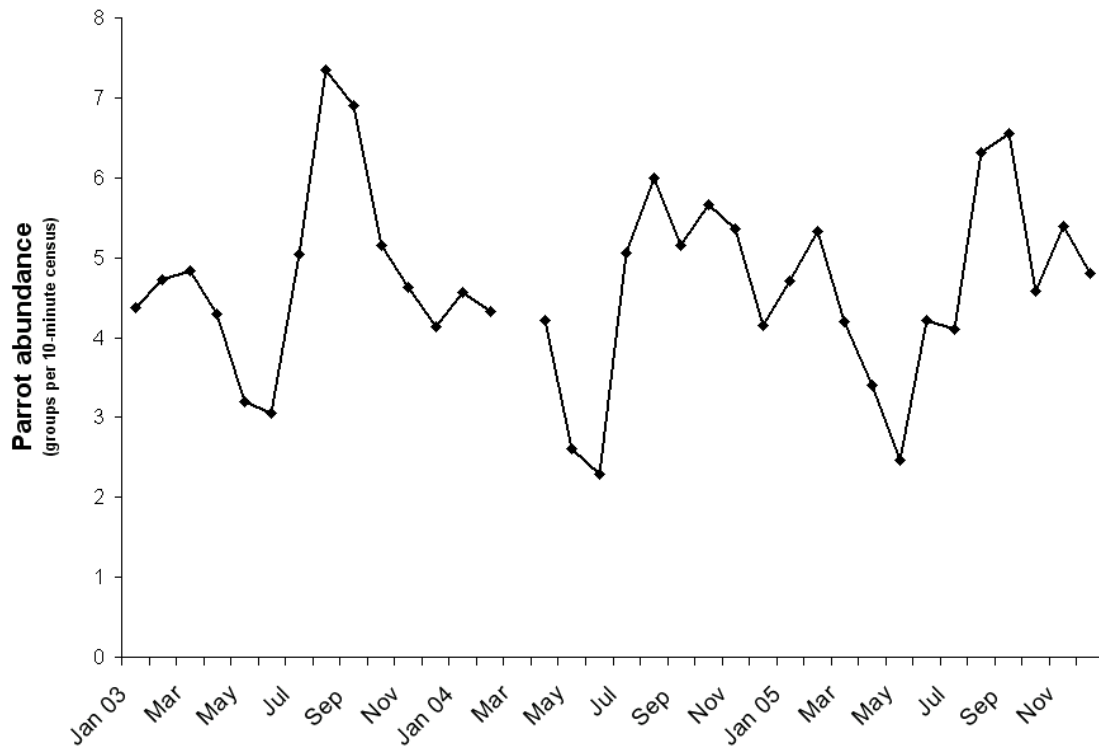
Figure 2: Parrot abundance in the forests surrounding Tambopata Research Center, Peru. Data represent the average number of parrot groups detected during each 10-minute point count.

Soil consumption

Data from 1,322 early mornings (< 7:30 AM) from January 2000 – August 2005 show a great deal of daily variation but broadly repeatable annual patterns. The annual low in lick use is in the early dry season (March – June, Fig. 3). The high season runs from the late dry season through the early wet season (August – January). All 12 parrot species that use the lick regularly show a strong seasonal peak in lick use. However, these peaks range from August to January depending on the species.
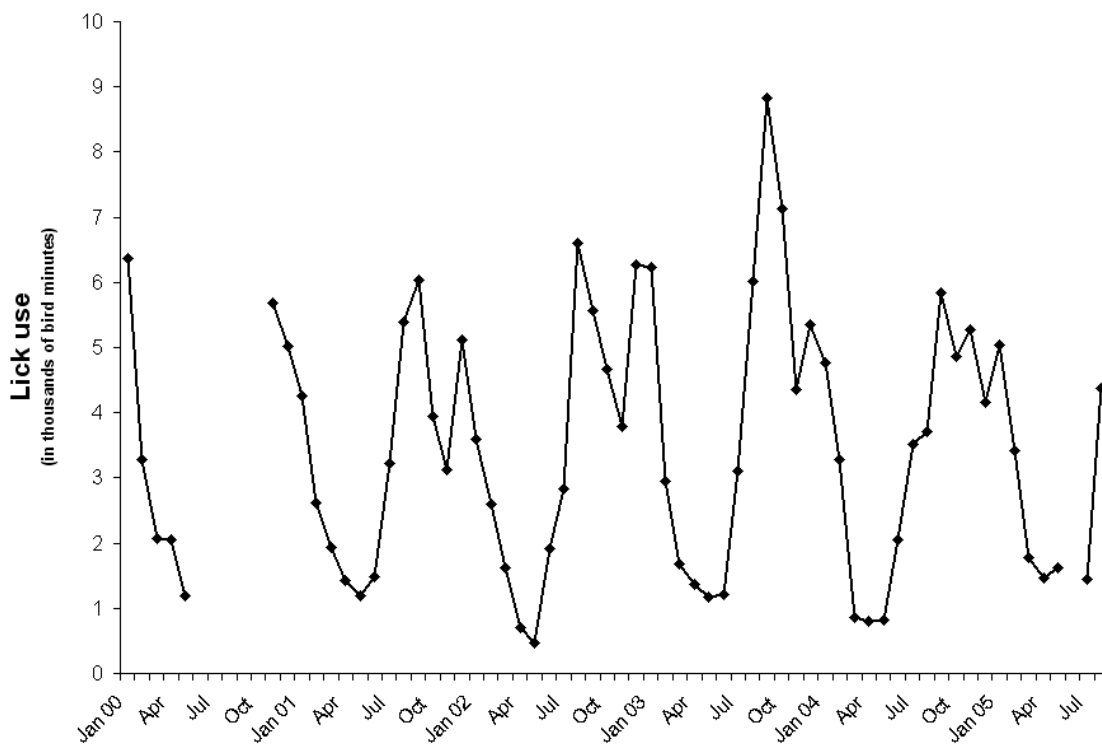

Figure 3: Clay lick use at Tambopata Research Center in southeastern Peru. Lick use represents monthly averages for all species of psittacines presented in thousands of bird minutes (5 birds on the lick for 10 minutes = 50 bird minutes). "Bird minutes" is used as a surrogate for the total amount of clay consumed.

Correlations among factors

The number of parrot species nesting in each month is significantly correlated with fruit and flower abundance (Spearman rank correlation on number of parrot species nesting per month and the percent of trees with flowers or fruits [data from all years combined], r = 0.78, P < 0.005, Fig. 1). The abundance of parrots at the site is weakly correlated with fruit and flower abundance (Spearman rank correlation on 14 monthly mean census figures and the percent of trees with fruits or flowers: r = 0.38, P < 0.1, Fig. 1). Clay lick use peaks during breeding season for all parrot species for which we have good information on nesting season and lick use. Clay lick use for all psittacine species is significantly correlated with their abundance (Spearman rank correlation on 30 monthly means of clay lick use and census data: r = 0.67, P < 0.001, Fig. 1).

Discussion

Psittacine soil consumption, abundance, and nesting show large seasonal variations in this highly diverse parrot community in the western Amazon basin. Flower and fruit abundance also show large seasonal changes in this area of tropical moist forest. While there is much variation in each data set, annual patterns are broadly repeatable, suggesting that these factors are not just driven by random events. While correlation does not prove causality, I will use the data presented here plus other data and information gleaned from the literature to develop a possible chain of causality that may be driving the annual parrot natural history cycles observed during this research.

Fruiting and flowering are lowest at the end of the wet season and peak in the early wet season. This pattern has been observed in other sites and may be driven by the annual rainfall patterns. Wind dispersed seeds often ripen in the late dry season when there are few leaves on the trees, the seed pods can dry out sufficiently, wind velocities are high in the canopy, and the dispersed seeds only have to wait a few months for the onset of the rains and the resulting good germination conditions (van Schaik et al. 1993). Fleshy fruit production usually peaks in the early wet season as there is abundant water available to form the fruits and allow immediate germination and growth. Producing seeds at the end of the wet season is considered sub optimal because the seeds and seedlings face a period of 7 months with reduced rainfall (van Schaik et al. 1993). The timing of the rains undoubtedly drives the pattern of flower and fruit abundance observed in this work in Tambopata.

Throughout the world, bird breeding is known to correlate with the period of highest food abundance (Lack 1968). This is because raising young (both pre and post fledging) requires a great deal of extra food. In our study, the seasonal abundance of flowers and fruits correlates significantly with the number of parrot species nesting each month. For this reason I feel that the seasonal abundance of food broadly dictates the timing of parrot reproduction in this system. Why smaller species nest earlier in the year than larger species is not immediately clear. However, smaller bodied species may be able to efficiently exploit smaller food sources (flowers, small unripe fruits, small wind dispersed seeds, etc.) than larger species. Further analysis of the tree phenology data and individual species' diets are needed and I predict that such smaller sized food sources will

be more common in the late dry season when the smaller parrot species nest. However smaller species are not known to nest earlier in other parrot communities so the relationship found here could be spurious (Roth 1984).

The finding that clay lick use correlates with breeding season for all parrot species was unexpected, as this had not been reported for parrots. However this pattern has been found for humans, bats, elephants, butterflies and a variety of other taxa (Arms et al. 1974; Holdo et al. 2002; Smedley & Eisner 1996; Wiley & Katz 1998). In these cases it is thought that the additional nutritional stress of reproduction is alleviated through nutrients from the soil. For humans it is hypothesized that the toxin binding properties of the soil may also help protect the developing fetus from toxins in the diet of the mother. Additional evidence for a direct link between soil consumption and parrot breeding comes from the finding that Scarlet Macaws regularly feed clay to their young at our site in Tambopata (DJB unpubl. data). As a result I feel that the observed pattern of increased clay lick use during the breeding season is driven, at least in part, by the adults consuming soil to bring to their nestlings.

Despite the clear link between clay lick use and breeding; there are apparently many non-breeding birds that visit the lick during the breeding season. I feel that this is the case for at least some of the species because their behavior around the lick strongly suggests that they are not breeding: 1) many pairs of Scarlet, Red-and-green, and Blue-and-yellow Macaws (*Ara ararauna*) arrive at the lick and spend hours and hours waiting above the lick, at the time when the females are brooding small chicks and don't leave the nest for

more than 5 to 15 minutes at a time, 2) flocks of over 100 Mealy Parrots and White-eyed Parakeets arrive in the early morning, suggesting that these birds slept in communal roosts, and not as pairs in isolated nests. At other seasons, like the end of the wet season and early dry season, these large flocks of parakeets and Amazons disappear. The census data also support the contention that there is a large influx of birds during the season of maximum clay lick use (Fig. 1).

In summary, the peak in clay lick use may be driven by two different phenomena: increased lick use by local breeding birds, and an influx of non-breeders. Why non-breeders should congregate near the lick is unclear, but could be related to an increase in general food supply. Under this scenario birds may congregate around the lick to take advantage of soil nutrients and the increased opportunities for social interaction in times of food abundance, and leave the area in times of food scarcity. Not all members of a species leave the area, in fact all of the common species are regularly recorded in all months. However, the abundance of individual species can vary drastically, as seen with Mealy Parrots whose abundance can drop by 87% within three months (DJB unpubl. census data).

The data presented here suggest that large numbers of psittacines move in and out of the study area annually (see also Karubian et al. 2005; Renton 2002). This is apparently in response to local fruiting and flowering patterns, which probably determine when each species nests and the local carrying capacity. Seasonally predictable movements to track available food supplies have been documented among other species of New World

Psittacines using radio telemetry: Lilac-crowned Parrots in Mexico (Renton 2001) Renton pers com.), Great-green Macaws in Costa Rica (Powell et al. 1999), and Mealy Parrots in Guatemala (Bjork 2004). In all these cases the birds ranged tens to hundreds of kilometers tracking food at the landscape level then returned to their nesting grounds the following year. Such large-scale movements create special challenges for conservation as birds frequently move out of official protected areas where they may be threatened by hunting, habitat loss, or trapping (Powell & Bjork 1995, 2004). Tambopata Research Center is located near the center of the 1.6 million ha Tambopata National Reserve – Bahuaja Sonene National Park. The results presented here beg the question "is this huge protected area big enough to protect the thousands of parrots that visit the clay lick annually?" Radio telemetry studies in nearby areas are working to determine the ranging requirements of macaws and parrots in the Amazon, and these may provide some answers.

Acknowledgements

Literature Cited

Adler, G. H., and K. A. Kielpinski. 2000. Reproductive phenology of a tropical canopy tree, *Spondias mombin*. Biotropica 32:686-692.

AOU 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Arms, K., P. Fenney, and R. C. Lederhouse. 1974. Sodium:stimulus for puddling behavior by tiger swallowtail butterflies, *Papilio glaucus*. Science 185.

Beissinger, S. R., and N. F. R. Snyder 1992. New World Parrots In Crisis. Smithsonian Institution Press, Washington, D.C.

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

Bjork, R. 2004. Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning. Wildlife Science. Oregon State University.

Brightsmith, D. J. 2004. Effects of weather on avian geophagy in Tambopata, Peru. Wilson Bulletin 116:134 -145.

Brightsmith, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. Wilson Bulletin 117:296-305.

Brightsmith, D. J., and R. Aramburú. 2004. Avian geophagy and soil characteristics in southeastern Peru. Biotropica 36:534-543.

Burger, J., and M. Gochfeld. 2003. Parrot behavior at a Rio Manu (Peru) clay lick: temporal patterns, associations, and antipredator responses. Acta Ethologica 6:23 - 34.

Casagrande, D. G., and S. R. Beissinger. 1997. Evaluation of four methods for estimating parrot population size. Condor 99:445-457.

Collar, N. J. 1997. Family Psittacidae. Pages 280-479 in J. d. Hoyo, A. Elliott, and J. Sargatal, editors. Handbook of the Birds of the World. Lynx Edicions, Barcelona, Spain.

Croat, T. B. 1975. Phenological behavior on Barro Colorado Island. Biotropica 7:270-277.

Dunning, J. B. 1993. CRC handbook of avian body masses. CRC Press, London.

Emmons, L. H. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. Biotropica 16:210-222.

Emmons, L. H., and N. M. Stark. 1979. Elemental composition of a natural mineral lick in Amazonia. Biotropica 11:311-313.

Forshaw, J. M. 1989. Parrots of the world. Landsdowne Editions, Melbourne, Australia.

Forshaw, J. M. 2006. Parrots of the world: an identification guide. Princeton University Press, Princeton, NJ.

Foster, R. B., T. Parker, A, A. H. Gentry, L. H. Emmons, A. Chicchón, T. Schulenberg, L. Rodríguez, G. Larnas, H. Ortega, J. Icochea, W. Wust, M. Romo, C. J. Alban, O. Phillips, C. Reynel, A. Kratter, P. K. Donahue, and L. J. Barkley. 1994. The

Tambopata-Candamo Reserved Zone of southeastern Peru: a biological assessment. Page 184. Conservation International, Washington, D.C.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparitive phenlogical studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881-919.

Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Science. USA 85:156-159.

Gilardi, J. D., S. S. Duffey, C. A. Munn, and L. A. Tell. 1999. Biochemical functions of geophagy in parrots: detoxification of dietary toxins and cytoprotective effects. Journal of Chemical Ecology 25:897-922.

Griscom, B. W., and P. M. S. Ashton. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in southeastern Peru. Forest Ecology and Management 175:445-454.

Holdo, R. M., J. P. Dudley, and L. R. McDowell. 2002. Geophagy in the African elephant in relation to availability of dietary sodium. Jounal of Mammalogy 83:652-664.

Karubian, J., J. Fabara, D. Yunes, J. P. Jorgenson, D. Romo, and T. B. Smith. 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. Condor 107:617-626.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lugo, A. E., and J. L. Frangi. 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. Biotropica 25:73-84.

Marsden, S. J. 1999. Estimation of parrot and hornbill densities using a point count distance sampling method. Ibis 141:377-390.

Marsden, S. J., and A. Fielding. 1999. Habitat associations of parrots on the Wallacean

    islands of Buru, Seram, and Sumba. Journal of Biogeography 26:439-446.

Marsden, S. J., M. Whiffin, L. Sadgrove, and P. G. Jr. 2000. Parrot populations and

    habitat use in and around two Brazilian Atlantic forest reserves. Biological

    Conservation 96:209-217.

Masello, J. F., M. Luján Pagnossin, C. Sommer, and P. Quillfeldt. 2006. Population size,

    provisioning frequency, flock size and foraging range at the largest known colony

    of Psittaciformes: the Burrowing Parrots of the north-eastern Patagonian coastal

    cliffs. Emu 106:69-79.

Masello, J. F., and P. Quillfeldt. 2002. Chick growth and breeding success of the

    burrowing parrot. Condor 104:574-586.

Montambault, J. R. 2002. Informes de las evaluaciones biológicas de Pampas del Heath,

    Perú, Alto Madidi, Bolivia, y Pando, Bolivia. Conservation International.,

    Washington, D.C.

Nycander, E., D. H. Blanco, K. M. Holle, A. d. Campo, C. A. Munn, J. I. Moscoso, and

    D. G. Ricalde. 1995. Manu and Tambopata: nesting success and techniques for

    increasing reproduction in wild macaws in southeastern Peru. Pages 423-443 in J.

    Abramson, B. L. Spear, and J. B. Thomsen, editors. The large macaws: their care,

    breeding and conservation. Raintree Publications, Ft. Bragg, CA.

Powell, G., P. Wright, U. Aleman, C. Guindon, S. Palminteri, and R. Bjork. 1999.

    Research findings and conservation recommendations for the Great Green Macaw

    (*Ara ambigua*) in Costa Rica. Centro Cientifico Tropical, San Jose, Costa Rica.

Powell, G. V. N., and R. Bjork. 1995. Implications of intratropical migration on reserve design: a case study using *Pharomachrus mocinno*. Conservation Biology 9:354 - 362.

Powell, G. V. N., and R. Bjork. 2004. Habitat linkages and the conservation of tropical biodiversity as indicated by seasonal migrations of Three-Wattled Bellbirds. Conservation Biology 18:500-509.

Räsänen, M. W., and A. M. Linna. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269:386-390.

Räsänen, M. W., and J. S. Salo. 1990. Evolution of the western Amazon lowland relief: impact of Andean foreland dynamics. Terra Nova 2:320-332.

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

Renton, K. 2002. Seasonal variation in occurrence of macaws along a rainforest river. Journal of Field Ornithology 73:15-19.

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

Roth, P. 1984. Repartição do habitat entre psitacídeos simpátricos no sul da Amazônia. Acta Amazonica 14:175 - 221.

Sanz, V., and A. Rodríquez-Ferraro. 2006. Reproductive parameters and productivity of the Yellow-shouldered Parrot on Margarita Isalnd, Venezuela: a long-term study. Condor 108:178-192.

Smedley, S. R., and T. Eisner. 1996. Sodium: a male moth's gift to its offspring. Proceedings of the National Academy of Science. USA 93:809-813.

Snyder, N. F. R., P. Mc Gowan, J. Gilardi, and A. Grajal. 2000. Parrots. Status survey and conservation action plan 2000-2004. Page 180 pp. IUCN, Gland, Switzerland and Cambridge, UK.

Terborgh, J., J. W. Fitzpatrick, and L. H. Emmons. 1984. Annotated checklist of birds and mammals species of Cocha Cashu Biological Station, Manu National Park, Peru. Fieldiana (Zoology, New Series) 21:1 - 29.

Terborgh, J., S. K. Robinson, T. A. P. III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213-238.

Tosi, J. A. 1960. Zonas de vida natural en el Perú. Memoria explicativa. sobre el mapa ecológico del Perú. Instituto Interamericano de las Ciencias Agriicolas de la Organización de los Estados Americanos.

van Schaik, C. P., J. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24:353-377.

Wiley, A. S., and S. H. Katz. 1998. Geophagy in pregnancy: a test of a hypothesis. Current Anthropology 39:532-545.

Zhang, S. Y., and L. X. Wang. 1995. Comparison of three fruit census methods in French Guiana. Journal of Tropical Ecology 11:281-294.

Appendix: Names of parrots referred to in the text. English names follow American Ornithologist's Union Checklist of North American birds (AOU 1998) supplemented by recent changes in Forshaw (2006). Taxonomic order follows Forshaw (2006). Aviculture names are those used commonly in aviculture according to the author's own experience. Latin names in [brackets] represent old genus or species names that have been changed recently. Subspecific identifications were made on the basis of the maps presented in Forshaw (2006) and were not confirmed with specimens. Subspecific names are listed only when the subspecies present in Tambopata are not the nominate subspecies.

English	Aviculture	Latin
Blue-and-yellow Macaw	Blue-and-gold Macaw	*Ara ararauna*
Scarlet Macaw		*Ara macao*
Red-and-green Macaw	Green-winged Macaw	*Ara chloropterus*
Chestnut-fronted Macaw	Severe Macaw	*Ara severus*
Red-bellied Macaw		*Orthopsittaca [Ara] manilata*
Blue-headed Macaw		*Primolius [Ara] couloni*
Red-shouldered Macaw	Noble Macaw	*Diopsittaca [Ara] nobilis longipennis*
White-eyed Parakeet	White-eyed Conure	*Aratinga leucopthalmus callogenys*
Dusky-headed Parakeet	Dusky Conure	*Aratinga weddellii*
Red-crowned Parakeet	Painted Conure	*Pyrrhura rosiefrons [picta]*
Black-capped Parakeet	Black-capped Conure	*Pyrrhura rupicola sandiae*
Dusky-billed Parrotlet	Sclater's Parrotlet	*Forpus sclateri*
Amazonian Parrotlet		*Nannopsittaca dachilleae*
Cobalt-winged Parakeet		*Brotogeris cyanoptera*
Tui Parakeet		*Brotogeris sanctithomae*
Scarlet-shouldered Parrotlet		*Touit huetii*
White-bellied Parrot	White-bellied Caique	*Pionites leucogaster xanthomeria*
Orange-cheeked Parrot	Barraband's Parrot	*Pionopsitta barrabandi aurantigena*
Blue-headed Parrot	Blue-headed Pionus	*Pionus menstruus*
Yellow-crowned Parrot	Yellow-crowned Amazon	*Amazona ochrocephala nattereri*
Mealy Parrot	Mealy Amazon	*Amazona farinosa*