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SENTINEL BEHAVIOR OR VIGILANCE AT A MACAW CLAYLICK?

Alan Tristram Kenneth Lee[1,2]

[1] Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, UK

[2] Current address: FitzPatrick Institute of African Ornithology, DST–NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

E-mail: alan.tk.lee@googlemail.com

Abstract · Sentinel behavior (co-ordinated vigilance) has been observed for a range of bird species living in family groups, usually in arid environments, but the behavior has never been formally identified for parrots. Riverside claylicks are sites where parrots and other species congregate to consume soil, usually in large numbers. Birds feeding on the clay are vulnerable to attack from predators. The Red-and-green Macaw *Ara chloropterus* can be observed in the vicinity of claylicks for much of the morning, although they spend only a small amount of time feeding on the clay itself. I investigated patterns of vigilance at a riverside claylick in Peru to test whether or not the birds engage in true sentinel behavior. There was no evidence for coordination of vigilance, and overall vigilance increased with the presence of more birds on the claylick, contrary to expectation. In addition, tall perches that should serve as sentinel positions were generally occupied less when birds were feeding on the claylick, and the probability of birds on the clay increased with increasing group size. Probability of calling, which could include warning information, was not higher as a function of bird presence on the clay, but was best explained by group size. All macaws maintained a generally high state of vigilance in the vicinity of the claylick, suggesting there was no reliance on a sentinel system. Further work is needed to understand the dynamics of this behavior for this species at one of southeastern Peru's most important ecotourism resources.

Resumen · Comportamiento de centinela o vigilancia en un sitio de colpa de guacamayos? El comportamiento de centinela (es decir la vigilancia coordinada) ha sido registrado para diversas especies de aves que viven en grupos familiares, en especial en ambientes áridos, pero este comportamiento no ha sido descripto para especies de loros y guacamayos. Los sitios de colpa a la vera de los ríos, son lugares donde loros y otras especies se congregan para consumir tierra y minerales, a menudo en grandes números. Las aves en los sitios de colpa son vulnerables a depredadores. El Guacamayo Aliverde (*Ara chloropterus*) puede ser encontrado en los alrededores de sitios de colpa durante gran parte de las mañanas, pero solo una fracción de tiempo es empleada en consumir tierra. En este trabajo investigué los patrones de vigilancia del Guacamayo Aliverde en un sitio de colpa en Perú, para determinar si estos son compatibles con comportamiento de centinela. No encontré evidencia a favor de un sistema coordinado de vigilancia, y en general la vigilancia aumento con el número de individuos en el sitio de colpa, en contra de las predicciones. Además, las perchas altas de vigilancia fueron usadas en menor medida cuando había individuos alimentándose en el sitio de colpa y la probabilidad de que hubiera individuos alimentándose en la colpa fue proporcional al número total de individuos en el área. La probabilidad de vocalización, que podría incluir información de alerta, no estuvo afectada por la presencia de individuos alimentándose, pero si con el total de individuos presentes en el área. Todos los guacamayos se mantuvieron en general en un estado de alerta alta en los alrededores del sitio de colpa, lo que sugiere que no dependían de un sistema de centinelas. Se requieren más trabajos para entender las dinámicas comportamentales en sitios de colpa, uno de los recursos turísticos más importantes del sudeste de Perú.

Key words: Behaviour · Clay-licking · Geophagy · Parrot · Psittacine · Sentinel behavior · Vigilance

INTRODUCTION

Sentinel behavior can be described as coordinated vigilance within social groups where individuals take turns acting as a look-out for danger (McGowan & Woolfenden 1989), and is characterized by staying in areas with

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clear views of the surrounding area in a high state of vigilance on the alert to danger (Bednekoff 1997, Wright et al. 2001). Sentinel behavior is distinct from vigilance, which only includes the presence of vigilant animals watching for predatory activity and not the coordination of vigilant individuals: vigilance occurs in most species of birds and mammals (Yasukawa et al. 1992). Individual sentinels fluctuate but, in general, the overall number of sentinels present at any given time is fairly steady (Bednekoff & Woolfenden 2006). Sentinels usually make sentinel calls so as to inform foragers of their presence (Manser 1999).

Sentinel behavior has been documented in a variety of taxa including, probably most famously, the meerkat (*Suricata suricatta*)(Manser 1999), and other mammals (Horrocks & Hunte 1986, Rasa 1986, Kotler et al. 1999). The avian literature on sentinel behavior includes mostly species outside the Neotropics, primarily in arid habitats (Wright et al. 2001, Bell et al. 2009, Yasukawa & Cockburn 2009, Hollén et al. 2011, Ridley et al. 2013, Walker et al. 2016, Ostreiher & Heifetz 2017), with the exception of Jungle Babblers (*Turdoides striatus*) (Gaston 1977). Most of these studies have addressed sentinel behavior in the context of nesting territory or flock foraging, but not in the context of an aggregation site. Sentinel behavior in parrots has not been previously reported (Bednekoff 2015).

Riverside geophagy sites (claylicks), where hundreds of individuals from upwards of ten species of parrot and other bird species congregate to consume clay, are important sources of sodium in a sodium-poor environment (Powell et al. 2009, Lee et al. 2010, Dudley et al. 2012). Tourist visits to these have become important components of rainforest ecotourism packages in southeastern Peru (Brightsmith et al. 2008). One of the most common parrot species at riverside claylicks across South America is the Red-and-green Macaw (*Ara chloropterus*) (Lee et al. 2010). Unlike most other parrot species that feed on clay in the early morning, these macaws are present in highest numbers from mid-morning to early afternoon, depending on the claylick location (Brightsmith 2004).

Weighing 1230 g and measuring up to a meter from head to tail (Forshaw 2006), Red-and-green Macaws are the third largest of the seventeen macaw species. In South America, they are found in lowland Amazon rainforest and temperate deciduous forest, with a large range of over ten million km^2 (BirdLife International 2017). They are classified as Least Concern, although populations have been reduced in parts of their range due to overharvesting for the pet trade (Juniper & Parr 1998). They are widespread in captivity, as they are socially interactive with both people and other parrots (Abramson et al. 1995). They are regarded as common in lowland Amazon rainforest, with published abundance for the species ranging from 1.8 to 8 individuals/km^2 (Terborgh et al. 1990, Haugaasen & Peres 2008, Lee & Marsden 2012). Pairs of macaws defend nest sites viciously (Renton & Brightsmith 2009), but form social foraging flocks and are seen in large numbers at claylicks (Emmons & Stark 1979, Brightsmith 2004). However, if sentinel behavior occurs in this species, it would be unusual because it is not associated with defense of a breeding territory or a closely-knit group of related-individuals that typically forages together (Bednekoff 2015).

Sentinel behavior studies are normally facilitated by the researchers' ability to identify individuals or distinctive sentinel positions (e.g., Newbold et al. 2008). However, since macaw sexes are alike and there are few physical characteristics that allow instantaneous identification of individual wild macaws, we explore sentinel behavior by looking at the vigilance patterns of the aggregation of macaws. If sentinel behavior occurs at a claylick we would predict the following: (1) Given that sentinels generally occupy high perches, there should always be vigilant birds in the highest band of vegetation while birds are consuming soil on the claylick; and furthermore, numbers on high perches should be constant, or at least not decrease, when there are birds on the soil; (2) If coordination of vigilance is taking place, the proportion of time intervals with no birds vigilant should be lower when birds are on the claylick compared to when no birds are on the claylick; (3) Overall vigilance may increase when birds are vulnerable if no birds are acting as sentinels; (4) The presence of birds on the claylick should be independent of total group size if sentinels are present at the pair or family group level; (5) The calling rates from birds high in the vegetation should increase when birds are on the claylick if this information encodes safety, coordination, or warning information, as predicted by the Watchman's hypothesis (Gaston 1977, Wickler 1985).

METHODS

Study area. The study area lies in the Madre de Dios Department of southeastern Peru, at the boundary between tropical moist and subtropical wet forest. Average elevation is 250 m a.s.l. and average rainfall 3200 mm (Brightsmith 2004). Surveys were conducted at a riverside claylick of the Las Piedras River (12°06'S, 69°52'W). The claylick where macaws fed was an approximately 20 m wide and 10 m high section of fluvial sediments of the western bank of the river.

Behavior monitoring. Observations were conducted on fifteen days, from 9 to 30 June 2011 and ten days from 7 to 16 September 2016. Observations were carried out from a blind from 05:30 h until usually 14:00 or 15:00 h if macaws were still around, with an observer team rotation between 10:00 and 10:30 h. Observers approached the blind concealed by the forest away from the claylick, and likely had little influence on the behavior of the birds in the vicinity of the lick. The observation point was 106 m from the surface of the claylick. The field of observation

from the researcher's vantage point extended to roughly 100 m on either side of the claylick, and to isolated emergent trees less than 100 m behind the claylick.

Data were collected by citizen scientists: 44 observers participated in data collection, each one participating in no more than four observation sessions, and in addition most observer pair or time combinations were unique. Observers ranged in age from 16 to 75 and were mostly from professional backgrounds. No observers considered themselves to be experts in macaws and only one described himself as a 'birder.' Observers were trained in macaw observation through provision of a training manual (Supplementary Material), a theory session (including imitation of behavior states), and one three-hour practical session at the claylick. Observers were not aware of the research hypotheses, only of the research protocol. This was done so as not to bias observations towards any particular behavior, or for any particular location around the claylick.

Using Swarovski 10x42 binoculars or 20–60x telescope, perch scans were conducted once every five-minutes using the group scan method with sequential instantaneous records of individual behaviors (Martin et al. 1993). An observer would scan all visible macaws in the vicinity of the claylick, starting with a horizontal scan of the high vegetation (at a level of about 15 m or higher); then scanning low (all vegetation below 15 m); and then the surface of the claylick. One observer described what the birds were doing to another person acting as recorder. The following behavior categories were recorded: vigilant, sleeping, resting, headshake, walking, calling, begging, regurgitation, playing, aggression, submission, fighting, preening, allopreening, scratching, branch biting, eating clay, defecating, kissing, mating, short flight, and departure flight. Descriptions of these are provided in the training manual provided to observers (Supplementary Material), but relevant categories for this article were: Vigilant ("Vigilance is how alert a bird is. A vigilant bird is actively looking around; head movement is notable, often with head twisted at 90 degrees from the body so that the bird is looking up at the sky or down at the ground. Neck is usually stretched"); 'Resting' ("Bird is perched with head low (towards the shoulders), usually looking forward, maybe looking slowly around, but not doing much else."); and Calling ("Bird is vocalizing – beak is open and call can be heard").

As previous research has shown that boat traffic can have an impact on bird behavior (Burger & Gochfeld 2003), all boats passing the claylick were recorded in five-minute intervals. Since weather can influence claylick use (Brightsmith 2004), no observations were made during rainy weather. Cloud cover was recorded to the nearest 25% (0 = clear, 100% = overcast).

Data analysis. The proportion of each behavior category was calculated by dividing the total number of observations for that behavior by the sum total of all behaviors scored, at the five-minute interval. Levels of vigilance of birds perched high in the vegetation were compared for when birds were on the claylick or not using the Wilcoxon rank sum test with continuity correction in R 3.1.3 (R Core Team 2015). To determine if total numbers of birds at high positions is constant despite the presence of birds feeding on the clay, a linear model predicting bird numbers as a function of birds on clay as a binary variable (presence/absence) was implemented.

To test coordination, the number of five-minute intervals with no vigilant birds high in the vegetation was compared relative to presence/absence of birds at the claylick using a chi-squared contingency table test using the GTest function from the DescTools package (Signorell 2017).

To explore overall patterns of vigilance for birds perched high in the vegetation, a generalized linear mixed model (glmm) was implemented with the lme4 package (Bates et al. 2013). The model examines the proportion of birds vigilant in the vegetation (arcsin transformed) as a function of boat presence, time of day represented by hour, total number of birds, number of birds on the claylick and cloud cover, using day as random effect. To indicate relative variable importance in model output tables, all results were scaled using the scale function in R. The random effect was included to account for any bias introduced by observer-pairs. Only data where four or more birds were present was used because we are interested in behaviour for groups of birds.

To determine if the presence of macaws on the claylick was independent of the total number of birds, the presence of birds on the claylick was modelled as a binomial variable (presence/absence) as a function of the total count of all macaws in the vegetation and calling rate using a logistic regression glmm, with day as random effect.

To further investigate call rate, calling was used as a binomial response (calling or no calling heard during the five-minute interval), as a logistic model better suited the low recording frequency of this behavior. Predictor variables were number of birds on the clay, cloud cover, hour, number of boats, the total number of birds present, and the proportion of birds scored as vigilant. Modelling was otherwise conducted as outlined for proportion of birds vigilant as described above.

RESULTS

Birds were scored most often as being vigilant (50%, n = 15,488 of 30,973 observation scores, Appendix 1), then preening (13%) and resting (6%). In contrast, begging, regurgitation and defecation were rarely observed (< 1%) and mating was never observed (Appendix 1). Social bonding interactions scored low (allopreening: 4%; kissing: 0.8%; playing: 0.8%), but far outscored antagonistic interactions (aggression: 0.3%; submission: 0.2%; fighting: < 0.1%). Feeding on

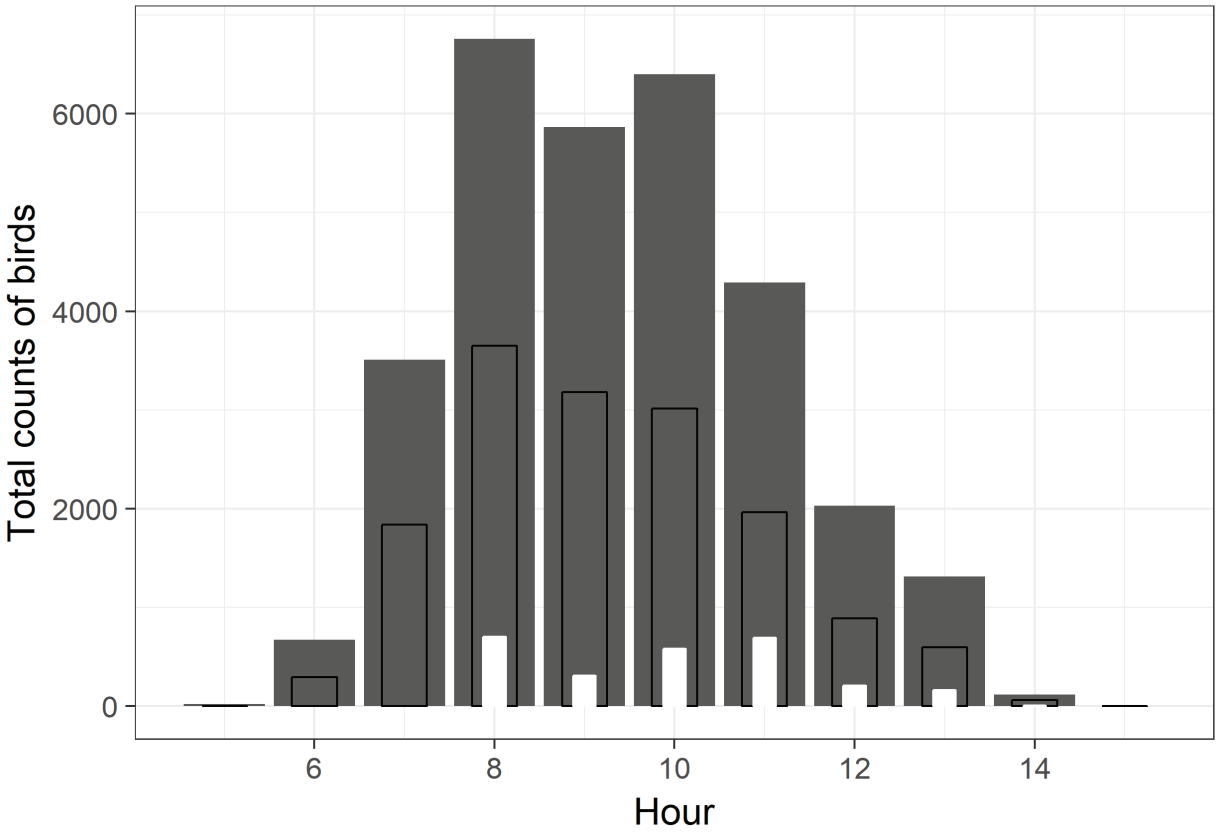

Figure 1. Summary daily Red-and-green Macaw (*Ara chloropterus*) activity at a claylick on the Las Piedras River, Peru, as indicated by counts of behavior scores. Grey bars indicate the sum total of all behavior scores of all observable birds around or on the claylick for each hour period across all observation periods. The black-inset bars represent the sum of all birds scored as vigilant. White bars represent the counts of birds on the surface of the clay, regardless of behavior type.

the clay typically occurred at mid- to late-morning (Figure 1).

There was no evidence that the macaws at this riverside claylick engaged in sentinel behavior, as evidenced by examining the results in the context of the five predictions.

1. The position of birds around the claylick: On 99% of scans while birds were on the clay, there were birds in the surrounding vegetation i.e. birds virtually never fed without the presence of other birds in the vegetation. This was not a function of space limitation on the claylick: the maximum number of birds observed on the surface of the clay was 54, while the mean was 14 (SD = 12). However, given that most birds were scored while perched high in the vegetation in the vicinity of the claylick, with fewest recorded on the claylick (high 64%, low 27%; clay 9%), it would have been unusual to observe no birds in this vegetation strata while birds were on the claylick. In addition, the numbers of birds in high positions was not independent of the presence of birds on the clay: fewer birds were observed high in the vegetation when more birds were on the clay (linear model estimate ± se: -1.94 ± 0.65, t = -2.95, P = 0.003, $F_{1,2732}$ = 8.73), despite the fact that one of the best predictors of bird presence on the claylick was the total number of birds (see below).

2. The proportion of five-minute time intervals without vigilant birds was not affected by the presence of birds on the clay (G = 1.64, df = 1, P = 0.2), suggesting no evidence for coordination of vigilance when birds were at their most vulnerable.

3. The amount of vigilance for birds high in the vegetation while birds were on the claylick: the proportion of vigilance displayed by macaws high in the trees was significantly higher when birds were on the clay compared to when birds were not on the clay (proportion of birds vigilant when birds on clay: 57 ± 23%; no birds on clay: 46 ± 30%; W = 170,454, P < 0.01). In addition, modelling vigilance as a function of birds on the clay, total birds, cloud cover, time and boat traffic, the strongest predictor was the presence of birds on the clay (Table 1: model output).

4. The probability of observing birds on the claylick was not independent of group size, but was in fact explained by increasing group size as indicated by the sum of birds across all layers of vegetation (Table 1). The probability of birds on the claylick was also explained by calling rate (Table 1), but overall calling rate was best explained by group size (see below).

5. The relation between calling birds and feeding on the claylick: The strongest predictor of increased probability of calling was the total number of birds present, while the numbers of birds present on the

Table 1. Models explaining the proportion of vigilance of birds in the vegetation (Modelling: Vigilance); probability of bird presence on the claylick (Modelling: Probability of birds on the claylick); and probability of calling (Modelling: Probability of calling), at a claylick on the Las Piedras River, Peruvian Amazon. Variables are scaled to facilitate interpretation of relative importance of contributing predictor variables. *P* values lower than 0.05 are highlighted in bold.

Coefficients	Estimate	SE	*t* value	*P* value
Modelling: Vigilance				
Intercept	0.52	0.03	7.4	< 0.01
Number of birds on clay	0.03	0.01	3.5	**< 0.01**
Cloud cover	-0.03	0.014	-2.3	**0.02**
Hour (time of day)	0.03	0.001	3.1	**0.001**
Boats	-0.002	0.008	-0.3	0.80
Modelling: Probability of birds on the claylick				
Intercept	-2.11	0.33	-6.4	< 0.01
Sum of birds in vegetation	0.67	0.06	10.4	**< 0.01**
Calling rate	0.18	0.05	3.5	**< 0.01**
Modelling: Probability of calling				
Intercept	-1.51	0.19	-7.8	< 0.01
Birds on clay	-0.11	0.07	-1.6	0.11
Cloud	-0.31	0.13	-2.5	**0.01**
Hour (time of day)	0.37	0.08	4.4	**< 0.01**
Total birds	0.51	0.08	6.4	**< 0.01**
Proportion of birds vigilant	-0.35	0.09	-3.9	**< 0.01**
Boats	0.06	0.07	0.9	0.37

claylick was not a significant predictor of call rate (Table 1). Call rate increased as the day progressed. Call rate was negatively associated with the number of birds scored as vigilant (Table 1).

DISCUSSION

Birds at claylicks are vulnerable to a wide variety of predators. While direct attacks were not observed during this study, in September 2016 we found evidence of a Mealy Parrot (*Amazona farinosa*) predated by an ocelot (*Leopardus pardalis*) in the vicinity of the claylick. Predation of parrot species at claylicks by ocelot, Orange-breasted Falcon (*Falco deiroleucus*), and Ornate Hawk-Eagle (*Spizaetus ornatus*) have been observed elsewhere (Lee 2010). In addition, we observed one event of hunting from a passing boat, when birds were fired upon by an individual with a shotgun.

Despite dangers associated with regular aggregation at the claylick, this observational study provides little support that sentinel behavior occurs with Red-and-green Macaws. Parrots are rarely members of mixed species flocks in the Amazon, and none have been identified as 'sentinel species' in that context (Munn 1984, Alvesl & Cavalcanti 1996). Sentinels often use elevated perches or positions in the landscape (Bednekoff 2015). Although there were almost always birds in the vegetation when there were birds on the claylick, observations indicated these were simply preferred perch locations, prior to or after feeding on the clay.

The key difference between vigilance and sentinel behavior is the coordination of vigilance within a group (Bednekoff 2015). The proportion of birds vigilant was higher for birds in the vegetation when birds were on the clay compared to when no birds were on the clay, contrary to what would be expected if there was reliance on a single sentinel. If sentinel birds were present, vigilance should be constant (Bell et al. 2009), and increased overall vigilance suggests birds are looking out for themselves rather than relying on sentinels. It may be that the birds were not actively watching for predators, but perhaps were just watching closely the activity on the claylick. That this heightened vigilance occurs would mean that birds which are unable to be vigilant on the claylick would gain a benefit from any alarm calls emanating from birds in the vegetation, a situation which can be considered to be by-product mutualism (Bednekoff 2001). Clearly, high levels of vigilance are needed in a dangerous environment made no friendlier by the incursions of man.

Should sentinel behavior occur for pairs or small family groups, then feeding should occur for small groups of birds as well as big groups of birds. Instead, the probability of macaw presence on the clay was best explained by the total number of birds present. This may be because of a reduction in individual predation risk through the group size effect whereby a

reduction in individual risk occurs for larger group sizes, through encounter, dilution and confusion effects (Roberts 1996). How macaws 'count' their own number at a claylick needs further study, but it may be that an indication of overall group size is given by call rates as this was also a predictor of bird presence on the claylick. Previous studies have found that individual vigilance declines as group size increases (Roberts 1996), but this was not observed in our study.

Lastly, the probability of calling overall was not predicted by the presence of the birds on the claylick, which ran contrary to our expectation because for some species, sentinels signal their vigilant behavior to other members of the group through distinct vocalizations (Gaston 1977). It may be that confirming whether a bird was vocalizing or not was perhaps beyond the capabilities of this set of observers; but in addition it is possible that we did not observe the set of circumstances necessary to increase call rate i.e. predator presence.

The benefits of sentinels to a group are clear. It has been shown that foragers who can see or hear sentinels are more likely to forage in high-nutrient areas with less consideration for the amount of cover or protection available (Manser 1999, Hollen et al. 2008). By contrast, for macaws coming to the ground and spending time in a vulnerable position, safety is enhanced by wider levels of vigilance of other individuals present. Birds which have fed or obtained clay from the claylick often perch in the vicinity of the claylick thereby superficially appearing to be sentinels.

In contrast to most studies that have detected sentinel behavior, this study from a mesic (rainforest) environment provides contrasting results. While macaws perched in tall trees around claylicks maintain high levels of vigilance, especially in high positions, it is unlikely that macaws stick to strict rotation of individuals. It is more likely that individuals are acting for their own benefit in accordance with the numbers and behaviors of the birds around them. To strictly test for sentinel behavior of macaws or other parrots, marked individuals would be required to monitor the rotation of feeding through the flock.

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Appendix 1. Summary of the various behaviors scored during observations of Red-and-green Macaws (*Ara chloropterus*) at a claylick on the Las Piedras River, Peruvian Amazon. Behaviors are summed for across the observation period (Total), and broken down into strata of where the birds were perched where this information was available. CLAY is on the surface of the claylick, LOW is below 15 m within the vegetation, and HIGH is for birds perched > 15 m in the vegetation. Percentage values for total indicate the percentage of the behavior across all behavior types, while percentage for the strata indicate what percentage of the behavior occurred for each behavior across the strata.

Behavior	Total	Percentage	HIGH	Percentage	LOW	Percentage	CLAY	Percentage
Vigilance	15488	50.0%	10153	66%	4740	30%	590	4%
Preening	3646	11.8%	2776	76%	867	24%	3	0%
Resting	1989	6.4%	1277	64%	666	33%	46	2%
Short Flight	1851	6.0%	1127	61%	606	33%	118	6%
Walking	1817	5.9%	54	3%	114	6%	1649	91%
Allopreening	1378	4.4%	1005	73%	283	21%	86	6%
Calling	1284	4.1%	1111	87%	171	13%	2	0%
Branch-biting	925	3.0%	523	57%	350	38%	52	6%
Eating	640	2.1%	497	78%	129	20%	14	2%
Flight away	456	1.5%	306	67%	147	32%	3	1%
Scratching	282	0.9%	206	73%	71	25%	5	2%
Playing	250	0.8%	192	77%	57	23%	1	0%
Kissing	243	0.8%	140	58%	88	36%	15	6%
Wing-stretch	176	0.6%	142	81%	25	14%	9	5%
Panting	158	0.5%	138	87%	20	13%	0	0%
Sleep	129	0.4%	93	72%	32	25%	4	3%
Aggression	92	0.3%	35	38%	23	25%	34	37%
Headshake	67	0.2%	54	81%	13	19%	0	0%
Submission	60	0.2%	26	43%	18	30%	16	27%
Fighting	26	0.1%	13	50%	5	19%	8	31%
Begging	10	0.0%	10	100%	0	0%	0	0%
Regurgitation	4	0.0%	4	100%	0	0%	0	0%
Defecation	2	0.0%	1	50%	1	50%	0	0%
Copulation	0	0.0%	0		0		0	