Temporal variation in vertical stratification of neotropical bats

Comentado [ACAM1]: Suggestion: Segregation temporal in the vertical space for insectivores bats in the neotropical forest

Dylan G. E. Gomes[1*], Giulliana Appel[2], and Jesse R. Barber[1]

[1] Department of Biological Sciences, Boise State University, Boise, ID, USA 83725-1515

[2] Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus 69080-971, Brazil

Corresponding Author:

Dylan Gomes[1]

Email address: dylangomes@u.boisestate.edu

Abstract

Previous research has shown diverse vertical space use by various taxa, highlighting the importance of forest canopy. Yet, we often fail to explore how this three-dimensional space use changes over time. Our aim was survey the vertical space used by neotropical bats in French Guiana. Here we use passive acoustic monitoring in two canopy tower systems in French Guiana to monitor neotropical bat activity in canopy and understory throughout nine nights in the wet season. We show that different bats use both canopy and understory space differently, and that this can change throughout the night. We find that bats are overall more active in the canopy, but multiple species/acoustic complexes are more active in the understory. We also find that species that do not seem to prefer understory or canopy, when data are aggregated by night, do show temporally changing preferences in hourly activity. This work highlights the need to consider temporal axes in studies of space use, both throughout daily cycles and across seasons.

Comentado [ACAM2]: Aim of this study

Comentado [ACAM3]: Here you could include the hypothesis

Comentado [ACAM4]: Include key species

Comentado [ACAM5]: This exploration was only in 4 species and the before result was on 19 sp or complex.

Comentado [ACAM6]: Include family names or complex

Comentado [ACAM7]: All the bats or insectivores?

Introduction

The study of space use has long interested ecologists (Elton, 1927), and more recently three-dimensional space use has been shown to be important for many taxa including arthropods (Schulze, Linsenmair & Fiedler, 2001; Basset et al., 2003), birds (Pearson, 1971; Walther, 2002), rodents, marsupials (Vieira & Monteiro-Filho, 2003), and bats (Francis, 1994; Bernard, 2001). From an applied perspective, failing to survey animals above the forest canopy can lead to biased conclusions about management decisions. For example, European bats that have higher risk of wind turbine mortality were later found to be more common in higher vertical strata (Müller et al., 2013). Had we understood how these animals use space over time, we may have made different decisions about where to place wind turbines, and when to shut them down. Exploring how animals use vertical strata across time is important to understanding conservation strategies for forests and the animals that use that space. This is especially true in the tropics where biodiversity loss from deforestation is high (Laurance, 1999; Giam, 2017).

Comentado [ACAM8]: You can explore this new approach. Why is it important for this taxa?

Bats are ideal study organisms for exploring vertical stratification of space-use (cite). They comprise a group that is diverse, ecologically and economically important (Kalka, Smith & Kalko, 2008; Boyles et al., 2011; Kasso & Balakrishnan, 2013), highly sensitive to deforestation

Comentado [ACAM9]: Maybe, you can include some sentences about segregation spatial. For example: Kalko & Handley 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation, or Pereira et al 2010. Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Also the acoustic space in neotropicales bats, and the fluctuations of the resources in time and space. Foraging behavior in aerial insectivorous bats

(Garcia-Morales et al., 2016), and are relatively easy to monitor with recent advances in passive acoustic monitoring. Passive monitoring of tropical bats during the dry season suggests that bat activity and species diversity is higher in the canopy, relative to mid- or below-canopy (Marques, Ramos Pereira & Palmeirim, 2016). This may be a result of high insect abundance in the canopy (Basset et al., 2003). For example, many nectar feeding Lepidoptera (e.g. Sphingidae) are present in the canopy, where the flowers are more abundant (Schulze, Linsenmair & Fiedler, 2001). Yet, it is likely that vertical space uses by bats would vary throughout the night, and seasonally by the availability of resources in the space. Indeed, some tropical insectivorous bat species adjust their activity during the night to take advantage of more favorable periods to forage (Appel et al., 2019). Yet little is known about temporal patterns of vertical space use by aerial insectivorous bats. Here we survey the vertical space used by neotropical bats in French Guiana.

Methods

Data collection

We sampled above and below two canopy towers, part of the COPAS infrastructure, at the Nourages research station, French Guiana (coordinates) from 10 April 2018, to 19 April 2018 (n= x hrs) in the wet season. We conducted paired sampling on top of the canopy towers (~ 40 m high), to get a measure of activity above the forest canopy, and below canopy towers (~1.5 m high), to get a measure of bat activity in the forest understory.

At each sample site, we deployed a passive acoustic monitoring unit (Song Meter SM3) with an omnidirectional ultrasonic microphone (SMU; Wildlife Acoustics, Massachusetts, USA). We programmed acoustic monitors to run continuously from sunset to sunrise (~12 hours) and to record with a 16-bit depth, 384 kHz sample rate, with an internal 16 kHz high pass filter, and a 1.5 ms minimum trigger duration.

Sonar sequence identification

Bat recordings were batch processed with Sonobatch scrubbing software to exclude non-bat calls (cite). We then visualized the remaining 16,123 sequences with Kaleidoscope Software (version

Comentado [ACAM10]: Include some sentence about What is new advance in the methods.
See: Gibb et al. 2018. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods in Ecology and E

Comentado [ACAM11]: I consider important that this topic be further explored, because this study is about space partitioning through the time

Comentado [ACAM12]: Here you could include the hypothesis and the predictions of this study.

Eliminado: over the course of the entire night, for nine nights.

Comentado [ACAM13]: could be overlap of records for both microphones (canopy and understory)?, For example, a bat emit calls in canopy, is possible record this call in the understory?, this maybe a problem because you can register a presence in understory when in fact it is not.

Eliminado: the evening of

Eliminado: the morning of

Comentado [ACAM14]: include the total of hours of acoustic sampling

Comentado [ACAM15]: please, include min and max of canopy and understory

Comentado [ACAM16]: please, add distances between towers, habitat description: maximum canopy height, forest cover, climate data (temperature and rainfall).

Comentado [ACAM17]: Include the frequency range for this exclusion

Comentado [ACAM18]: Please, cite the software.

Eliminado: ,

4.3.2; Wildlife Acoustics, Massachussetts, USA) and identified the calls following and compare the calls with echolocation literature for Amazonian bats (López-Baucells, 2018), for the French Guiana (Barataud et al., 2013) and Brazil (Arias-Aguilar et al., 2018). When possible, we identified bat calls to the species level or identified the call as an acoustic complex when species-level identification was impossible (Torrent et al., 2018). Our analysis included a total of 19 sonotypes from the families Emballonuridae, Molossidae, Mormoopidae and Vespertilionidae (Table 1). We defined bat activity as the number of bat passes per hour, and night. A bat pass is a sequence of 5-s recording that has a minimum of two recognizable search-phase calls per species (Torrent et al., 2018; Appel et al., 2019).

Statistical analysis

Generalized linear mixed-effects models (GLMMs; cite method) were used to test our models using a Bayesian framework with the function xxxx in the package `rstanarm` (Gabry & Goodrich, 2016) in R Software (R Core Team, 2017). Our data was transform to xxxx o not xxx. follow data processing protocol of Zuur e Ieno 2016.

The aim of this analyses was evaluated if the bat activity changes through the night and between strata (canopy and understory). Our fist model was xxxxx

We visually checked model residuals and trace plots, and inspected predictors for collinearity. There were no divergent transitions or issues with convergence. All priors were uninformed.

and the model selection criterion was (BIC or DIC)…

the second model was …

Since all response data were counts of bat passes, we modelled these data with a negative binomial distribution and log link function. In our 'all bats' model (presented in Figs 1 and 2) we set a random (varying) intercept for bat species, with varying slopes for hour after sunset (0-12), vertical strata (canopy vs understory), and the interaction between the two (which were also fitted as fixed effects to make inferences on 'all bats' overall). We did not include site as a random effect, as we did not have at least five levels (Harrison et al., 2018).

Comentado [ACAM19]: Through a visual inspection of the call shape, number and energy of harmonics, Peak frequency, call duration, call interval …..

Comentado [ACAM20]: What was the criteria for the groups?

Comentado [ACAM21]: The table 1 has more than 19 sonotypes.

This information should be in the table 1.

Comentado [ACAM22]: I didn't find the results about it. Where is the results by species and strata?

Eliminado: a total of 11 species and eight acoustic complexes, with a total of 19 sonotypes from the families Emballonuridae, Molossidae, Mormoopidae and Vespertilionidae

Comentado [ACAM23]: Please, read Zuur & Ieno 2016 https://besjournals.onlinelibrary.wiley.com/doi/epdf/10.1111/2041-210X.12577 and use it to describe your models. Also, Stanton 2017. Reasoning with data: an introduction to traditional and Bayesian statistics using R.

Please, include the if the data was transformed or not for the models (mean is 0 and sd 1). Zuur, Ieno & Elphick (2010) provide a comprehensive guide on using data exploration techniques to check model assumptions, and give advice on transformations.

Comentado [ACAM24]: Include the specific function

Eliminado: that we ran in

Comentado [ACAM25]: Describe your model and draw the equation

Comentado [ACAM26]: You can include the plots in an appendix.

Movido (inserción)[1]

Comentado [ACAM27]: Include the function and the results of the collinearity.

Movido hacia arriba[1]: We visually checked model residuals and trace plots, and inspected predictors for collinearity. There were no divergent transitions or issues with convergence. All priors were uninformed.¶

We included horizontal moon illumination (measured following Kyba, Conrad & Shatwell, 2020) as a fixed effect to control for any influences that moon light might have on vertical bat activity (Hecker & Brigham, 1999; Appel et al., 2017), as well as any latent processes occurring over the course of the nine-day experiment (either due to moonlight or day of the year). In this model, we removed all bat species (or acoustic complexes) that contained 5 or fewer observations, since these data are not robust enough for inference.

Comentado [ACAM30]: Provides a more detailed description of how to sampling these measures in the study area. Also, a question is that Kyba et al. said that horizontal illuminance is a weak predictor to the impact of moonlight on animal physiology and behavior.

Comentado [ACAM31]: What was the experiment?

Eliminado: nine day

To further elucidate patterns of bat activity over the course of the night, we separately analyzed the four most common bat species (*Peropteryx macrotis*, *Saccopteryx bilineata*, *Centronycteris maximiliani*, and *Peropteryx kappleri*) with hour after sunset as a second-order polynomial, vertical strata (canopy vs understory), and the interaction between the two all fitted as fixed effects in a generalized linear model.

Comentado [ACAM32]: Did you find differences between nights for bat activity?

Comentado [ACAM33]: The most common in the area, or the most common in canopy, or understory? Is not clear how do you got this conclusion, please describe better.

We did not run similar models because the number of calls was small for sp1 (n=), sp2, sp3 …, and the inferences on minimal data were not appropriate (cite).

Comentado [ACAM34]: Did you do a statistical analysis (n samples) ?, or maybe include a number of calls by species is more clear. What was the n for every strata?

https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12541 (Smaller effect size in models)

Eliminado: for other species, as we did not feel like we had an adequate number of counts for those species

Throughout the results we report 80% and 90% credible intervals from a Bayesian framework. While these choices are always largely arbitrary, we chose these values because both display a wide interval spanning a high probability range of parameter values (cite). We avoid using a 95% credible interval because firstly these can often be misinterpreted as 95% confidence intervals. The latter, in contrast to Bayesian credible intervals, assumes that the interval is random, and the parameter is fixed, and are often interpreted as a hypothesis test (cite). Secondly, both 80% and 90% credible intervals reduce concerns with the computational stability of wider (e.g. 95%) intervals. In the following text we generally use 80% CI to suggest broad-scale trends, whereas we use 90% CI in the reporting of parameter estimates, to give a narrower estimate band, with higher certainty.

Results

Comentado [ACAM35]: the outputs of the models are missing

I suggest to write a paragraph with the general results of the bat passes, how many bat passes in canopy and understory? (t-Test), How many passes was excluded of the analysis? What was the bat activity trough the nights? Was different by night and strata?

Overall, bats were more active in the canopy, versus the understory. That is, bat activity was estimated to be 9.5 times (90% CI: 4.3 – 21.1) higher in the canopy, than in the understory. Yet, patterns for individual species (or acoustic complexes) were mixed (Fig 1). Broad patterns at 80% credible intervals suggest six species/complexes are more active in the canopy, five in the understory, and six aren't more or less active in any particular strata. Of the strongest trends, *Peropteryx macrotis* was 21.8 times more likely to be found in the canopy (90% CI: 6.01 – 84.6), whereas *Myotis riparius* was a factor of 132.8 more likely to be in the understory (90% CI: 31.2 – 586.6). There was a 92.2% probability that moonlight has a positive effect on overall bat activity, but we did not have the data resolution to look at individual species effects.

Overall bat activity decreased 22.0% (90% CI: 14.8 – 29.6%) for every hour in the canopy as the night progressed, whereas activity in the understory did not change over time (90% CI: -8.2 – 10.7%). Individual bat species/complexes differed in their activity above and below the canopy as the evening progressed, depending on the species/complex (Fig 2). Three bat complexes increased understory use over the night, whereas none of them decreased their use of that space over time (90% CI). The *Lasiurus sp.* complex, for example, was 52.5% more active in the understory (90% CI: 32.4 – 83.1), each hour of the night (Fig 2). Canopy use throughout the night, however, increased for two groups, and decreased for one at the 90% CI, but trended that direction for two other groups (80% CI; Fig 2). Two of the complexes (Molossidae group A & B) increased the use of both understory and canopy throughout the night.

Centronycteris maximiliani activity showed a peak of activity in the middle of the night. This species is slightly more active in the understory, relative to the canopy, during early and late parts of the night, whereas they are more active above the canopy during the middle of the night (Fig 3A). *Saccopteryx bilineata* has higher activity in the understory at the beginning and end of the night (dusk and dawn), and higher canopy activity in the early-middle of the night (Fig 3B). Both *Peropteryx kappleri* and *P. macrotis* are far more active above the canopy (relative to understory), but there is a small, difficult to visualize, spike in understory activity late in the night (Fig 3C, D).

Discussion

Comentado [ACAM36]: What species, please include the results of the bat activity for every strata.

For example: https://onlinelibrary.wiley.com/doi/epdf/10.1111/j.1461-0248.2004.00603.x Fig. 3.

Comentado [ACAM37]: Should be possible run a t-test to get a statistical difference?

Comentado [ACAM38]: Is more interesting if include the name of species.

Con formato: Subrayado

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Comentado [ACAM39]: How was measure this variable?

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Comentado [ACAM40]: I saw that in figure 3, you did simulations, then you need to describe them in methods.

Understanding space use over time is vital if we hope to accurately assess habitat use and quality for bats (Bernard, 2001; Müller et al., 2013; Appel et al., 2019). Since it is difficult to directly observe bats flying in the night, spatio-temporal resolution from passive acoustic monitoring may offer important insights about the natural history of bats, and ultimately their conservation (Marques, Ramos Pereira & Palmeirim, 2016). Here we show that both the canopy and understory are used differently by different neotropical bats, throughout the night.

We find that bats are overall more active in the canopy, which corroborates previous work (Marques, Ramos Pereira & Palmeirim, 2016) and that overall bat activity decreases in the canopy throughout the night. We also find multiple species that are more active in the understory (only *Myotis riparius* in Marques, Ramos Pereira & Palmeirim, 2016). Other Myotid species are thought to prefer to forage in the understory elsewhere in the world (Kennedy, Sillett & Szewczak, 2014; Wellig et al., 2018), suggesting that this characteristic may be a trait of the genus independent of the geographic location.

It is possible that some differences between this study and Marques et al. (2016) are explained by seasonal differences in prey communities within the canopy and understory, as this study was during the wet season and Marques et al. (2016) occurred during the dry season. Arthropod prey varies seasonally in their abundance (Wolda, 1988; Lister & Aguayo, 1992; Pinheiro et al., 2002) and those prey likely spend time in different vertical strata (Schulze, Linsenmair & Fiedler, 2001). Indeed, seasonal changes in arthropod abundances in the neotropics have been linked to changes in diets of many taxa, including bats (Lister & Aguayo, 1992; Jahn et al., 2010; Salinas-Ramos et al., 2015). However, there are likely many other idiosyncratic differences between the French Guiana and Brazilian forests studied here and in Marques et al. (2016), respectively, that could contribute to these differences as well. Future work should aim to understand three-dimensional space use over longer periods of time within the same forest.

~~For many bats, there were no clear preferences between canopy and understory (Fig 1). This may be because these bats are just as active in the various vertical strata.~~ Bernard (2001), for example, found the same lack of vertical stratification pattern as we did for *Saccopteryx bilineata* and *S. leptura*, and the author suggests that this may be because these species fly in large spiral movements occupying both the higher and lower strata. Instead, this apparent lack of a pattern may suggest that bats partition the night and are more active in different strata at different times.

Comentado [ACAM41]: In the samplings only insectivores are present? Some particular family in canopy or understory?

Comentado [ACAM42]: the use of Bayesian glmms makes it difficult to compare with other studies that address this topic (use of vertical space) with frequentist approach for example Marques et al. 2016

Comentado [ACAM43]: Maybe the morphology of wings and the habitat structure

Comentado [ACAM44]: Write, what are the differences?

Comentado [ACAM45]: I didn't find specific information about it in the text.

Comentado [ACAM46]: You can discuss more the differences between time through the night (moon light) and resources like insects, more than seasonality, because you don't have how discuss seasonality.

Comentado [ACAM47]: Write the species

Con formato: Tachado

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Comentado [ACAM48]: What species, is better is you include the specific names.

Comentado [ACAM49]: rewrite

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S. bilineata provides an example, as they were not more active in either stratum when their activity was integrated over the entire night (Fig1), yet they partition their use of the canopy and understory across the night. *S. bilineata* has a "U"-shaped change in activity in the understory over time. This suggests that these bats roost somewhere near our detectors, likely inside tree cavities and on exposed trunks (Voss et al., 2016), but spend the middle hours of the night foraging above the canopy (Fig 3B). If bats are virtually non-existent in a survey of the understory during early hours of the night, but common in the canopy during later hours, it is likely that they are roosting elsewhere and commuting to forage (Voss et al., 2016).

With the constant increase of deforestation of Amazonian primary forests (Fearnside, 2005; Lovejoy & Nobre, 2018) and consequent loss of vertical stratification of these forests (Silva et al., 2020), aerial insectivorous bat activity is being affected by forest removal and degradation. Delineating specifically how vertical structure shapes bat communities and activity adds critical insight for ecologists and managers (CITE). Here we show that monitoring for bats in one vertical stratum only, or during just the early 'golden' hours of the night clearly misses important information. ~~On the more speculative side, given enough information about a species' emergence timing (Rydell, Entwistle & Racey, 1996; Duvergé et al., 2000; Russo, Cistrone & Jones, 2007),~~ it may even be possible to estimate distances to roosts from these data. If this were the case, multiple passive acoustic monitors scattered throughout a forest could roughly triangulate on the location of these roosts (Svaizer, Matassoni & Omologo, 1997; Chang et al., 2002), which could then be preferentially protected from deforestation or development.

Conclusions

We used passive acoustic monitoring to explore how neotropical bats use space over time. While bats generally were more active in the forest canopy, we show that individual groups of bats use space differently over the course of a night. Those who fail to survey habitat in three dimensions, and for the entire duration of a night may form erroneous conclusions about the quality of that habitat, or make poor management decisions. We hope that future work continues to explore how animals and their prey use space throughout the night, and over the course of different seasons, which will surely expand our knowledge of these understudied creatures.

Comentado [ACAM50]: You can discuss more about it. For example, how is the foraging behavior in aerial bats, the species are edge space, open space, narrow space. The wing shape can to influence where they flight, or the space segregation. Has Emballonuridae species an acoustic characteristic that allow a capture efficient of insects in one of this strata?.

Comentado [ACAM51]: see references

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Comentado [ACAM52]: Be more specific

Comentado [ACAM53]:

Acknowledgements:

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Comentado [ACAM54]: Journal, pp, vol.

Con formato: Resaltar

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	Family	Sonotypes	Understory	Canopy	Total
1		*Peropteryx trinitatis*	0	1	1
2		*Pteronotus sp.*	0	1	1
3		*Saccopteryx gymnura*	1	0	1
4		*Diclidurus sp.*	2	3	5
5		*Molossus molossus*	0	20	20
6		*Pteronotus gymnonotus*	2	19	21
7		*Pteronotus rubiginosus*	20	15	35
8		*Lasiurus blossevilli / Rhogeessa Io*	0	37	37
9		*Lasiurus sp.*	69	3	72
10		*Phyllostomidae*	13	84	97
11		*Myotis riparius*	203	2	205
12		*Myotis simus/nigricans*	143	88	231
13		*Molossidae group B*	55	198	253
14		*Molossidae group A*	57	214	271
15		*Pteronotus alitonus*	362	4	366
16		*Cormura brevirostris*	10	379	389
17		*Saccopteryx leptura*	397	671	1068
18		*Peropteryx kappleri*	280	1264	1544
19		*Centrontcteris maximiliani*	1270	944	2214
20		*Saccopteryx bilineata*	1018	3512	4530
21		*Peropteryx macrotis*	70	4692	4762

Con formato: Ancho: 27,94 cm, Alto: 21,59 cm

Comentado [ACAM55]: Maybe include the mean and sd of the number passes for every sonotype for every strata.

Comentado [ACAM56]: How did these species complex? Any particular peak frequency?

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
1		DAY	HOUR	X	COLOR	POS	Bat	Number	Date	Time	S.Az	S.Alt	M.Az	M.Alt	Phase	M.SD	S.Illm	M.Illm	T.Illm
2	1	10	0	1	green	above	cen1	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
3	2	10	0	2	green	above	corbre	6	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
4	3	10	0	3	green	above	dic.sp	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
5	4	10	0	4	green	above	mol1	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
6	5	10	0	5	green	above	mol2	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
7	6	10	0	6	green	above	molossidae3	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
8	7	10	0	7	green	above	myorip	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
9	8	10	0	8	green	above	myosp	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
10	9	10	0	9	green	above	perkap	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
11	10	10	0	10	green	above	permac	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
12	11	10	0	11	green	above	pertri	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
13	12	10	0	12	green	above	phyllo	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
14	13	10	0	13	green	above	pteali	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
15	14	10	0	14	green	above	ptegym	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
16	15	10	0	15	green	above	pterub	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04
17	16	10	0	16	green	above	ptesp	0	04/10/2018	00:00	326.22	-75.59	108.07	-32.23	0.326	0.246	0	0	5,00E-04

Comentado [ACAM57]: In the data more information are necessaries:

Number is ….? number or pass, or calls ..

Time or hour, explain the difference or the reason for both cols.

Color…?
S.Az is….?
S. Alt…?
…

Please include the units. (Kiloherzt., Hertz, miliseconds, seconds)

Also, the values of the measure of T.Illm are big differences. Why ? for example, 0.0005; 19.794; 8400