

25 **Abstract**

26 Relative humidity (RH) was measured at hourly intervals for approximately one year
27 in two caves at seven stations near Playa del Carmen in Quintana Roo, Mexico.
28 Sistema Muévelo Rico is a 1.1 km long cave with 12 entrances and almost no dark
29 zone. Río Secreto (Tuch) is a large river cave with more than 40 km of passages,
30 and an extensive dark zone. Given the need for cave specialists to adapt to
31 saturated humidity, presumably by cuticular thinning, the major stress of RH would
32 be its deviation from saturation. RH in Río Secreto (Tuch) was invariant at three sites
33 and displayed short deviations from 100% RH at the other four sites. These
34 deviations were concentrated at the end of the nortes and beginning of the rainy
35 season. Three of the sites in Sistema Muévelo Rico showed a similar pattern
36 although the timing of the deviations from 100% RH was somewhat displaced. Four
37 sites in Sistema Muévelo Rico were more variable, and were analyzed using a
38 measure of amount of time of deviation from 100% RH for each 24 hour period.
39 Strong seasonality was evident but, remarkably, periods of constant high humidity
40 were not the same at all sites. In most Sistema Muévelo Rico sites, there was a
41 detectable 24 hour cycle in RH, although it was quite weak in about half of them. For
42 Río Secreto (Tuch) only one site showed any sign of a 24 hour cycle. The
43 troglomorphic fauna was more or less uniformly spread throughout the caves and did
44 not concentrate in any one area or set of RH conditions. Compared to temperature,
45 RH is much more constant, perhaps even more constant than the amount of light.

46 Introduction

47 The transition from a surface habitat to the subterranean habitat of caves is a
48 profound one, both physically and biologically. At least three physical attributes of
49 caves change significantly. Light disappears, or at least nearly so—there is at least
50 the theoretical possibility of light in a cave. Badino [1] showed Cerenkov radiation
51 emitted in air, water and rock by cosmic ray muons resulted in light production in
52 caves, and in at least some large chambers, should be detectable by the human eye.
53 Temperature variation is greatly reduced, and hovers around the mean annual
54 surface temperature [2,3]. Relative humidity, the focus of this contribution, does not
55 behave as does temperature, but rather increases, and in many cases, remains near
56 saturation [3,4], well above mean annual relative humidity on the surface.

57 A cave entrance is a transition zone (ecotone) between the illuminated
58 surface environment and the constant darkness of the subsurface. The transition
59 between light and dark is not necessarily abrupt and nearly all caves have a twilight
60 zone of reduced, but not absent, light. In some exceptional cases, some light is
61 present throughout the cave, even when the cave is more than 1000 m in length [1].
62 Beyond the twilight zone is a zone of fluctuating temperature [2], followed by a zone
63 of constant temperature [3]. The zone of fluctuating temperature may also be
64 extensive and it is not entirely clear whether most caves do in fact have a constant
65 temperature zone [4].

66 Of these three physical factors, relative humidity has received the least
67 attention. Culver and Pipan [5] argue that light is the only driver of convergent natural
68 selection in subterranean habitats. The biological importance of cave temperature is
69 less obvious but even small differences in temperature, on the order of 1° C, can
70 have a major impact on micro-distribution of cave spiders, and an important feature

71 of niche differentiation among competing species [6,7]. Relative humidity is perhaps
72 the most constant of the three, and Howarth [4,8] argues that it is of profound
73 importance as a selective factor, and that the ability of a terrestrial organisms to
74 survive in an atmosphere of 100% RH requires major morphological changes,
75 especially cuticular thinning. Howarth [8] showed that longevity for the Hawaiian
76 spider *Lycosa howarthi* was reduced by 25% as a result of a RH drop to only 90%
77 from saturation. Hadley et al. [9] further showed that the cuticle of cave spiders was
78 thinned, compared to surface relatives. This reduction allows individuals to survive
79 water saturated environments, but at a cost of desiccation when relative humidity
80 drops below saturation [8,9]. As they point out, at 100% RH, the subterranean
81 terrestrial environment has some features of an aquatic environment and is certainly
82 an extreme environment.

83 Each of these three factors is mediated through cave entrances and has a
84 spatial distribution of values that in the deep cave is invariant, or at least assumed to
85 be invariant. For temperature, the presumed invariant value is the mean annual
86 surface temperature [3,10], for light it is its absence, and for relative humidity it is
87 saturation (or more properly vapor equilibrium pressure [10]). The length of the cave
88 until the invariant zone is reached depends on the particular geometry of the cave,
89 particularly with respect to the size and aspect of the entrance(s) [11].

90 In a previous study [12], we analyzed both spatial and temporal variation in
91 temperature in three caves in Quintana Roo, Mexico, and found a remarkable
92 amount of cyclical variation (both daily and annual) in temperature, both in photic
93 and aphotic zones. The daily signal in some aphotic sites was extremely weak, but
94 the annual cycle had an amplitude of at least 2° C. Cropley [13] reported a minimum
95 of 4° C variation in sites 1800 m from the entrance in two large cave systems in West

96 Virginia. Likewise, Šebela and Turk [14] found 1° C of variation at sites deep in the
97 Postojna Planina Cave System of Slovenia. There may well be zones of constant
98 temperature in these large caves, but the zone of variable temperature is extensive.

99 Relative humidity in caves, the focus of this study, has been little investigated,
100 either theoretically or empirically, in comparison. There is a rich literature on cave
101 temperatures, including topics such as mean temperature prediction using passage
102 size, entrance size and exterior temperature [15]; time lags between exterior and
103 cave temperature [16,17]; the relationship between ventilation and temperature [18],
104 as well as general analytical treatments [10,16].

105 In an analytical sense, relative humidity is less interesting than temperature in
106 part because it is so dependent on temperature—the vapor equilibrium pressure
107 depends on the temperature of the system and the vapor equilibrium pressure (g/m^3)
108 is numerically close to the temperature in °C [10]. Badino [10] further suggests that
109 humidity is generally at saturation (equilibrium) when in close contact of water
110 surfaces and air. However, RH is interesting biologically because of the apparent
111 sensitivity of cave organisms to even small deviations from saturation [4,8,9]. It is
112 also of geochemical interest because it is the switch point between evaporation and
113 condensation. For example, carbonate dissolution can occur via condensation
114 corrosion in saturated air [19].

115 Our goals in this study are:

- 116 1. Characterize the relative humidity regime, based on hourly samples taken
117 over a year, for a series of sites in two tropical caves.
- 118 2. Identify zones of constant humidity, and to characterize short term deviations
119 from saturated relative humidity in these two caves.
- 120 3. Detect daily and seasonal cycles in the two caves.

121 4. Compare humidity patterns with those of temperature and light.

122

123 **Materials and methods**

124 **The study caves**

125 The two caves (Sistema Muévelo Rico and Río Secreto) are located in the
126 Quintana Roo in the Yucatan Peninsula (Fig 1) in an area with one of the highest
127 cave densities of cave passages (mostly flooded) in the world [20,21]. Air filled caves
128 are also numerous and they are constrained to a relatively thin layer of flat-bedded
129 limestone with a depth of 5 to 10 m to the water table, and a surface topography of
130 gentle ridges and swales with an overall relief of 1-5 m [20,22] The area has an
131 annual cycle of precipitation characterized by three seasons: nortes (cold front
132 season between November and February), dry season (March to May), and rainy
133 season (June to October) which is the hurricane season [23]. During the rainy
134 season 70% of the precipitation occurs. The annual mean air temperature is 25.8° C
135 and the overall precipitation at Playa del Carmen averages 1500 mm [23].

136

137 **Fig 1. Locator map for caves and sampling sites in the two caves.** Maps
138 courtesy of Peter Sprouse. From: Mejía-Ortíz et al. [12].

139

140 Sistema Muévelo Rico (20°32'05.1"N, 87°12'16.5"W) is located near the
141 settlement of Paamul, in the Mexican state of Quintana Roo (Fig 1). Its surveyed
142 length is 1151 m with a vertical extent of only 4 m [21]. Sistema Muévelo Rico has a
143 large number of entrances, more than 12, if skylights are included. Because of the
144 close proximity of the water table to the surface, vertical development and

145 subterranean terrestrial habitats are very restricted. The cave, with an elevation of 7
146 m at the entrance, is less than 2 km from the Caribbean Sea. There were seven
147 monitoring points in the cave. It was originally chosen for study because of its
148 extensive twilight zone and extremely small aphotic zone [24].

149 Río Secreto (20°35'27"N, 87°8'3"W) is a shallow, horizontally developed cave
150 with 42 km of surveyed passages (Fig 1) . It is a tourist cave and the tours are
151 conducted in a small section of the cave. The main entrance is 5 km from the
152 Caribbean coast and 12 km NE of Sistema Muévelo Rico. Tides can affect the water
153 table in Río Secreto up to several cm [23]. There were seven monitoring points
154 clustered in the vicinity of the Tuch entrance (Fig 1), and we refer to the cave as Río
155 Secreto (Tuch) throughout.

156 Taken together, the two caves represent two very different cave
157 environments—relatively large with numerous surface connections (Sistema
158 Muévelo Rico) to very large and less connected with the surface (Río Secreto
159 [Tuch]).

160

161 **Relative humidity measurement**

162 Relative humidity (along with temperature, see Mejía-Ortiz et al. [12,24]) was
163 measured at hourly intervals for the following dates:

- 164 • Sistema Muévelo Rico—5 April 2015 to 28 March 2016, n= 8593
- 165 • Río Secreto (Tuch entrance)—25 September 2018 to 26 October 2019, n =
166 9515

167 Onset Computer Corporation HOBO™ U23 Pro v2 data loggers were used to
168 measure relative humidity, and readings were accurate to $\pm 5\%$ for RH above 90%,
169 with a resolution of 0.05%. However, we found that accuracy was better than

170 reported. Nearby sensors and temporally nearby measurements were consistent to
171 more than 0.1% RH. Eight sensors were installed in Sistema Muévelo Rico, and one
172 failed. Seven sensors were installed in Río Secreto, and all functioned for the entire
173 measuring period.

174

175 **Faunal inventory**

176 A preliminary faunal inventory was done in Río Secreto (Tuch) by employing a
177 visual census for 30 person minutes at each station at the time the dataloggers were
178 installed. Species were identified to morpho-species and species with reduced eyes
179 and pigment (troglomorphs) were recorded. Previously analyzed data from Sistema
180 Muévelo Rico [24] was used for comparative purposes.

181

182 **Data analysis**

183 RH data from these two caves presented a number of statistical challenges.
184 First, the data are percentages and bounded by 100. Second, the large majority of
185 the values were 100, and for most stations, deviations from 100 were short-term,
186 typically lasting less than 24 hours, and thus there was a clear baseline of 100
187 percent, populated with short-term deviations. We created two types of variables.
188 First, in those cases where deviations were uncommon (all of the Río Secreto (Tuch)
189 sites and sites 3,6, and 7 in Sistema Muévelo Rico), we tabulated the number of
190 deviations of two hours or more from 100 percent for each month. Single hour
191 deviations were not tabulated to reduce noisiness in the data and to eliminate very
192 small deviations. Secondly, we created a daily variable for the remaining Sistema
193 Muévelo Rico sites that is the proportion of hourly measurements in a day that had

194 RH<100. For example, 0.2 means 20% of 24 measurements were less than 100%
195 RH. Using a generalized linear mixed model, we analyzed the proportion as a
196 binomial variable with an autoregressive autocorrelation of ar(1) and allowing excess
197 variance to vary among seasons. Mean daily RH itself was analyzed in a similar way
198 but did not meet the usual general linear model assumptions and yielded no
199 significant results (not reported here).

200 Basic statistics (means, minima, maxima, and coefficients of variation) were
201 calculated in EXCEL™, as were graphs of temporal patterns. Daily RH means were
202 also generated in EXCEL™ for comparison with mean surface RH from Cozumel Air
203 Force base, the closest monitoring point, which was approximately 20 km from the
204 caves. Generalized linear models were calculated in SAS v9.4 (SAS Institute, Inc.,
205 Cary, NC).

206 Spectral analyses were done on hourly data to detect possible (daily) cycles.
207 Cycles up to a period of 600 hours (25 days) were reported. Fisher's kappa tested
208 for deviation from white noise. Analyses were done using JMP® Pro 13.2.0 (©2016
209 SAS Institute, Inc. Cary, NC).

210

211 **Results**

212 **Overall Patterns**

213 The broad scale patterns of variation are summarized in Table 1. Mean RH at
214 all sites was greater than 97 percent, even at the entrance of Sistema Muévelo Rico,
215 and the lowest individual value was 69 percent, at the entrance to Sistema Muévelo
216 Rico. Two sites in Río Secreto (Tuch) showed no variation, and RH was always 100
217 percent at these sites. For five of seven sites in Río Secreto (Tuch), mean RH was

218 100% and for the other two, the mean was greater than 99.9% (Table 1). The
 219 percentage of time of deviation from 100% RH was always less than 2% Río Secreto
 220 (Tuch) and only above 50% in two sites in Sistema Muévelo Rico, including one right
 221 at the entrance. Variability, as measured by the coefficient of variation was always
 222 less for RH than for temperature. While the temporal variation in light was not
 223 measured, there were four sites with invariant absence of light. RH was more
 224 variable in Sistema Muévelo Rico, and mean RH was correlated with distance to an
 225 entrance (Fig 2).
 226

Table 1. Overall summary of RH data for Río Secreto (Tuch) and Sistema Muévelo Rico.

Cave	Station	Lux	Mean RH	Min RH	Max RH	Percent non-saturation	CV RH	CV Temp	N troglomorphic spp	Distance to entrance (m)
Sistema Muévelo Rico	1	<0.1	99.71	95.16	100	26.7	0.65	5.05	5	35
	2	<0.1	98.24	87.95	100	57.9	2.46	5.78	5	20
	3	<0.1	99.95	92.13	100	3.0	0.37	6.54	4	33
	4	<0.1	98.19	77.13	100	45.3	3.06	8.49	1	9
	5	466	97.06	69.12	100	52.7	4.53	9.82	3	0
	6	0.2	99.98	95.39	100	2.0	0.19	5.14	4	16
	7	<0.1	99.96	89.31	100	2.2	0.41	5.63	3	21
Río Secreto (Tuch)	1	0	99.99	90.97	100	0.4	0.18	3.70	4	17
	2	0	100	100	100	0.0	0.00	5.53	3	26
	3	0	100	100	100	0.0	0.00	5.13	2	8
	4	0	100	100	100	0.1	0.02	4.96	3	15
	5	<0.1	100.00	99.02	100	0.3	0.03	4.73	4	5
	6	0.8	100.00	96.49	100	0.3	0.06	6.27	3	9
	7	7.7	99.96	89.34	100	2.0	0.41	5.14	1	3

Non-saturation is defined as RH<0.995.

Light intensity in lux and the coefficient of variation for temperature at the same stations are shown for comparison. Light and temperature data are from Mejía-Ortiz et al. [12,24].

227

228

229 **Fig 2. Relationship between mean RH and distance from an entrance for**

230 **Sistema Muévelo Rico.** The linear regression is significant ($p=.041$, $R^2 = 0.60$), with
231 a slope of 0.07. Río Secreto (Tuch) showed almost no variation in mean RH at
232 different stations (Table 1).

233

234 The time courses for RH in the caves are very different from those of
235 surface RH at the nearby island of Cozumel (Fig 3). In the case of Río Secreto
236 (Tuch) surface RH was always lower, and there was not overlap of the RH curves for
237 the two sites, even when the most variable site in Rio Secreto (#7) was used for the
238 comparison. In the case of Sistema Muévelo Rico, overlap, even in the case of the
239 sensor placed right at an entrance (#5), RH overlapped only on a few days in May
240 and June, the end of the dry season for this sampling year.

241

242 **Fig 3. Comparison of cave and surface relative humidity.** Top: Daily average RH
243 (black line) for Río Secreto (Tuch) site 7 (the most variable site) and daily average
244 RH (gray line) for Cozumel for the period from 25 September 2018 to 26 October
245 2019. Bottom: Daily average RH (black line) for Sistema Muévelo Rico site 5 (the
246 most variable site) for the period from 5 April 2015 to 28 March 2016. Cozumel data
247 courtesy of Sub-lieutenant Jhosep Guadarrama Espinoza of Mexican Air Force
248 stationed in Cozumel.

249

250 **Seasonal pattern of RH**

251 The temporal pattern in Río Secreto (Tuch) was one of short downward
252 spikes (Fig 4), with three sites being invariant with respect to RH. The deviations

253 from 100% RH lasted between one and 49 hours, with most being only one or two
254 hours in duration. Only one lasted more than 24 hours. The spikes are concentrated
255 from September to January, in the end of the rainy season and start of the nortes
256 season (Fig 5). Most of the spikes were in the afternoon, and in half the cases, the
257 downward spike in RH was preceded by a slight rise in temperature. The one dry
258 season dip occurred at 10PM when temperature was dropping. Overall, there is a
259 weak seasonal pattern of constancy of RH outside the nortes season, where there
260 are short downward spikes in RH. Mean RH does not vary; only the frequency of
261 downward spikes varies.

262

263 **Fig 4. Variation in RH at the seven sites in Río Secreto (Tuch).** Site 7 is closest
264 to the entrance (see Table 1).

265

266 **Fig 5. Distribution of downward spikes in RH, by month, for sites in Río**
267 **Secreto (Tuch).**

268

269 The temporal pattern of RH in Sistema Muévelo Rico was more complicated
270 (Fig 6). Three of the sites—3,6, and 7—show the Río Secreto pattern of brief
271 downward spikes. However, their monthly distribution is different. Like Río Secreto
272 (Tuch), a number of spikes occur at the end of the Nortes season, but unlike Río
273 Secreto (Tuch), there is a second peak at the end of the dry season (Fig 7).

274

275 At the other four sites (1,2,4, and 5), downward spikes occur but there are
276 also extended periods where RH falls below 100 percent (Fig 6). Differences among
277 these sites and among seasons (nortes, dry, and rainy) were analyzed. Site,
season, and their interaction were all statistically significant (Table 2). According to

278 the model, the rainy season had the lowest frequency of deviations from 100% RH
279 and the dry season had the highest. The observed patterns, for the four individual
280 sites are more complicated (Table 3), indicating the importance of site by season
281 interactions (Table 2). In two sites (4 and 5), the nortes season showed the lowest
282 mean proportion of deviations for 100% RH, and at site 1, the nortes season showed
283 the highest mean proportion of deviations from 100% RH.

284

285 **Fig 6. Variation in RH at the seven sites in Sistema Muévelo Rico.**

286

287 **Fig 7. Distribution of downward spikes in RH, by month, for sites 3,6, and 7 in**
288 **Sistema Muévelo Rico.**

289

290 **Table 2. Type III test of fixed effects in linear generalized model for proportion**
291 **of hours not at 100% RH for four sites (1,2,4,5) in Sistema Muévelo Rico.**

Effect	Num DF	Den DF	F value	Pr>F
Site	3	38.08	3.20	0.034
Season	2	32.4	3.32	0.049
Site*Season	6	34.33	4.41	0.0021

292

293 **Table 3. Observed mean daily proportion of hours RH<100 by site and season**
294 **for Sistema Muévelo Rico.**

Site	Season	N Obs	Mean	Standard Error
1	Dry	85	0.12	0.03
	Nortes	121	0.69	0.04
	Rainy	153	0.01	0.004

2	Dry	85	0.98	0.01
	Nortes	121	0.68	0.04
	Rainy	153	0.28	0.03
4	Dry	85	0.69	0.05
	Nortes	121	0.18	0.03
	Rainy	153	0.53	0.03
5	Dry	85	0.72	0.05
	Nortes	121	0.23	0.03
	Rainy	153	0.65	0.03

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The differences in pattern cannot be explained by distance to the nearest entrance (Table 1). Those sites with the “Tuch” pattern of short term deviations from 100% RH are not the farthest from the entrance. Distance to an entrance only captures part of the extent of surface environmental influence, and size and aspect are also important, especially in Sistema Muévelo Rico, with multiple entrances.

Daily pattern of RH

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In the case of daily cycles in Río Secreto (Tuch), only sites 1,6, and 7 were variable enough to analyze for daily cycles. Although Fisher’s kappa test indicated the pattern was different from white noise, none of the three sites had a clear peak at 24 hours (Fig 8), with the possible exception of site 7.

309

310

Fig 8. Spectral analysis of sites 1,6, and 7 in Río Secreto (Tuch). All sites were significantly different from white noise, according to Fisher’s kappa test.

311

312 For Sistema Muévelo Rico, the results are shown in Fig 9. As expected, the
313 entrance station (#5) showed a very strong 24 hour signal, as did stations 2 and 4.
314 Stations 1 and 3 showed a relatively clear signal, but it was very weak. This is not
315 surprising since RH in the cave was invariant for about half of the year (Fig 7).
316 Stations 6 and 7 showed an even weaker signal, and they were also invariant for
317 much of the year.

318

319 **Fauna-RH connections**

320 The number of troglomorphic species, by station, is shown in Table 1. The
321 data for Sistema Muévelo Rico are the result of four censuses [24] and the data for
322 Río Secreto (Tuch) are the result of a single census, so comparisons between the
323 caves are not possible. In Río Secreto (Tuch), invariant or nearly invariant sites had
324 no more species than other sites. In Sistema Muévelo Rico likewise, variable RH
325 sites had no fewer species than invariant sites.

326

327 **Fig 9. Spectral analysis of cycles in RH at the seven monitoring stations in**
328 **Sistema Muévelo Rico.** Spectral density indicates the strength of the signal. Strong
329 cyclicity is seen at 24 hours. See also [24].

330

331 **Discussion**

332 **Patterns and variability of RH**

333 Relative humidity was less variable than temperature at all stations with
334 consistently lower coefficients of variation (Table 1). For seven sites in Río Secreto

335 (Tuch), three sites showed no variation in RH and the other four sites had
336 coefficients of variation of less than 1 percent. In Sistema Muévelo Rico, four sites
337 had coefficients of variation of less than 1 percent. No site in either cave had a
338 temperature coefficient of variation of less than 3.7 percent (site 1 in Río Secreto
339 (Tuch)).

340 While it was not possible to measure light more than once, the only aphotic
341 sites were four in Río Secreto (Tuch). The daily light-dark cycle at other sites may
342 result in coefficients of variation greater than 1 percent. In addition to the daily light
343 cycle, there is also a seasonal effect. Both the day length and apogee of the sun
344 vary seasonally. Day length ranges from 10 hr 51 min to 13 hr 25 min [24]. All of
345 this suggests that RH is less variable in these two caves than light, as well as
346 temperature.

347

348 **Seasonal and daily cycles of RH**

349 Seasonality of RH is present in both caves. In Río Secreto (Tuch), it is the
350 clustering of deviations from 100% RH at the end of the nortes season and the start
351 of the rainy season. In Sistema Muévelo Rico not only are there downward spikes,
352 but there are also extended periods of RH below 100%. However, these periods are
353 neither synchronous within the cave (Table 4) or with Río Secreto (Tuch) (Figs 4 and
354 6). This is in sharp contrast with the situation with temperature, where there was a
355 clear, synchronous seasonality [12]. Why there is more variability in RH at a small
356 spatial scale is unclear.

357 The daily pattern was one of diminished 24 hour periodicity compared to
358 temperature. In Sistema Muévelo Rico sites, a daily cycle could be detected at all

359 sites, albeit very weak in some. In Río Secreto (Tuch), a daily cycle was detectable
360 in only one site.

361

362 **Is there a winter effect?**

363 Numerous investigators have pointed out that in temperate caves there is a
364 “winter” effect, with a reduction in relative humidity, largely the result of air
365 movements [3,10,13,18,26]. According to Barr and Kuehne [27], these winter winds
366 resulted in the absence of cave fauna in affected passages in Mammoth Cave,
367 Kentucky. They only found animals in passages with RH above 94 percent, while
368 some passages had RH near 80 percent. Barr and Kuehne [27] used sling
369 psychrometer to measure RH and thus could only find RH away from walls, floors,
370 etc. In these sites, winds would be higher than along the substrate, and hence RH
371 would be lower. Howarth [8] argues that terrestrial cave limited invertebrates have
372 evolved to survive in 100 percent RH, a water saturated environment, by cuticular
373 thinning [9], which allows for greater water exchange. The cost of this adaptation is
374 water loss (and increased mortality) in non-saturated environments. Howarth [8]
375 points out that water saturated environments are in some ways aquatic habitats.

376 It is not at all clear that there is any winter effect in Río Secreto, and that it
377 appears diminished in Sistema Muévelo Rico. In Río Secreto, drops in RH, if they
378 occur at all, are of very short duration (Figs 3 and 4). Most of the short duration
379 downward spikes occur in the nortes season. In Sistema Muévelo Rico, there are
380 periods of RH that are below saturation for extended periods of time (Fig 6), but it is
381 unknown if the magnitude of the drops is sufficient to cause any physiological
382 response from the organisms inhabiting the cave. We found no discernible effect in
383 faunal composition through the seasons [24].

384 Furthermore, it is not at all clear how general the winter effect in temperate
385 zone caves is, and we know of no well documented RH measurements in a cave
386 throughout a year that show it. Tobin et al. [28] report near constant RH in a small
387 California marble cave but they did not monitor the cave from January through April.
388 Several authors [26,27,29] report both on RH variation and winds in Mammoth Cave,
389 but there are little quantitative data taken at regular intervals.

390 There are desert caves that are noticeably drier, but even in these cases, RH
391 is rarely less than 80 percent, even in dusty passages. Probably the best studied is
392 Torgac Cave in New Mexico [30]. The cave, developed in dolomite, is covered with
393 gypsum minerals, which are formed as a result of evaporation [31,32]. RH in the
394 cave in January ranged from 85 to 95 percent, both on the basis of sling
395 psychrometer and electronic sensor readings [30]. Unfortunately, no seasonal data
396 are available to know if RH is higher in the summer. The winter effect is understudied
397 in general and especially so in tropical caves.

398 Rather than a winter effect there may be a hurricane period effect, because
399 during hurricanes the humidity is close to 100 % outside, and the rain has several
400 effects on the energy sources, growth of roots, organic matter entrance, and of
401 course on the changes in the temperature and humidity.

402

403 **Comparison of patterns of RH, temperature, and light**

404 Typically, caves are divided into three zones [2,3,27,28]: (1) an entrance zone
405 with light, (2) an intermediate aphotic zone with variable temperature, and (3) a deep
406 zone without light and constant temperature. How relative humidity fits into this
407 scheme is not clear. In Río Secreto (Tuch), relative humidity was constant, or nearly
408 so, not only in the dark zone, but also at two stations with light present (4 and 5,

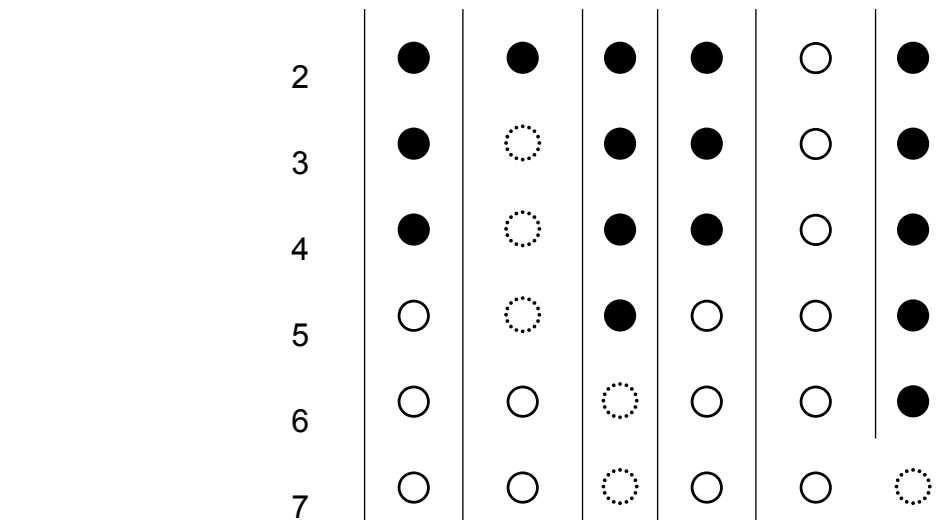
409 Table 2). In Sistema Muévelo Rico, which was chosen because of its extensive
 410 twilight zone and multiple entrances [24], only site 7 did not show a clear seasonal
 411 pattern (Fig 6), but the daily cycle was largely absent (Fig 7).

412 This pattern stands in sharp contrast with temperature. In Sistema Muévelo
 413 Rico, there was no zone of constant temperature and almost no zone of constant
 414 darkness (Table 4). Even in Río Secreto (Tuch), there was always a seasonal and
 415 daily cycle of temperature. It may well be that a constant temperature zone can be
 416 found deeper in the cave, the demonstration of a constant temperature zone in any
 417 cave remains elusive. Overall, 100 percent RH is more common than complete
 418 darkness, at least in the caves we studied.

419

Table 4. Presence/absence of variation in temperature, light, and relative humidity in the two study caves, by station.

Cave	Station	Daily Cycle			Seasonality		
		Light	Temp.	RH	Light	Temp.	RH
Sistema Muévelo Rico	1	○	○	○	○	○	●
	2	○	○	○	○	○	●
	3	○	○	○	○	○	⊙
	4	○	○	○	○	○	●
	5	○	○	○	○	○	⊙
	6	○	○	⊙	○	○	●
	7	○	○	⊙	○	○	⊙
Río Secreto (Tuch)	1	●	⊙	●	●	○	●



Black circles indicate an aphotic station, acyclic temperature, and acyclic RH. Dotted circles are cases where cyclicity is very weak.

420

421 **How biologically and geologically important is RH in** 422 **caves?**

423 RH is critically important in several geological processes. One of these
424 involves carbonate dissolution—condensation corrosion, the condensation of warm,
425 humid air to cold rock walls [19], which can be an important factor in speleogenesis
426 in some circumstances [31]. Mineral precipitation in caves, especially gypsum
427 minerals, is the result of evaporation [32]. Gypsum minerals can appear and
428 disappear seasonally as RH in cave passages changes.

429 Howarth [8] proposed that because of the high humidity of caves that
430 terrestrial species adapted by cuticular thinning which allowed for greater water
431 movement across the integument. This morphological difference was demonstrated
432 in the case of lycosid spiders living in lava tubes in Hawaii [9] and for a terrestrial
433 isopod, *Titanethes alba*, in Slovenian caves [33]. Interestingly, this species is
434 amphibious and can move in and out of water. Humphreys and Collis [34] showed
435 that cave arthropods from the Cape Range of Australia showed greater water loss

436 than epigean species presumably as the result of cuticular thinning. Cuticular
437 thinning may well be a very common convergent trait, and is certainly worthy of
438 further study.

439

440 **Supporting information**

441 **S1 Table. Hourly relative humidity data for Sistem Muévelo Rico. (XLSX)**

442 **S2 Table. Hourly relative humidity data for Río Secreto (Tuch). (XLSX)**

443

444 **Acknowledgements**

445 Alberto Rivero gave permission to visit the Sistema Muévelo Rico. Tania
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448 Guadarrama Espinoza from Mexican Air Force for providing the meteorological data
449 for Cozumel. No permits were needed since no organisms were collected for this
450 study.

451

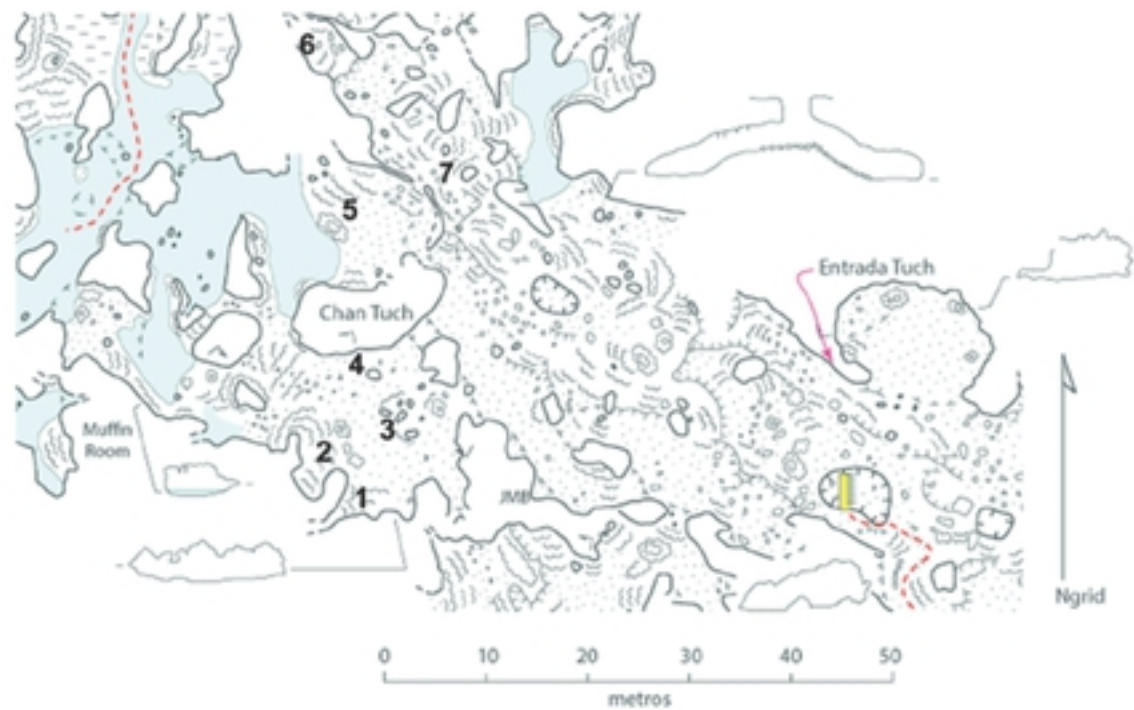
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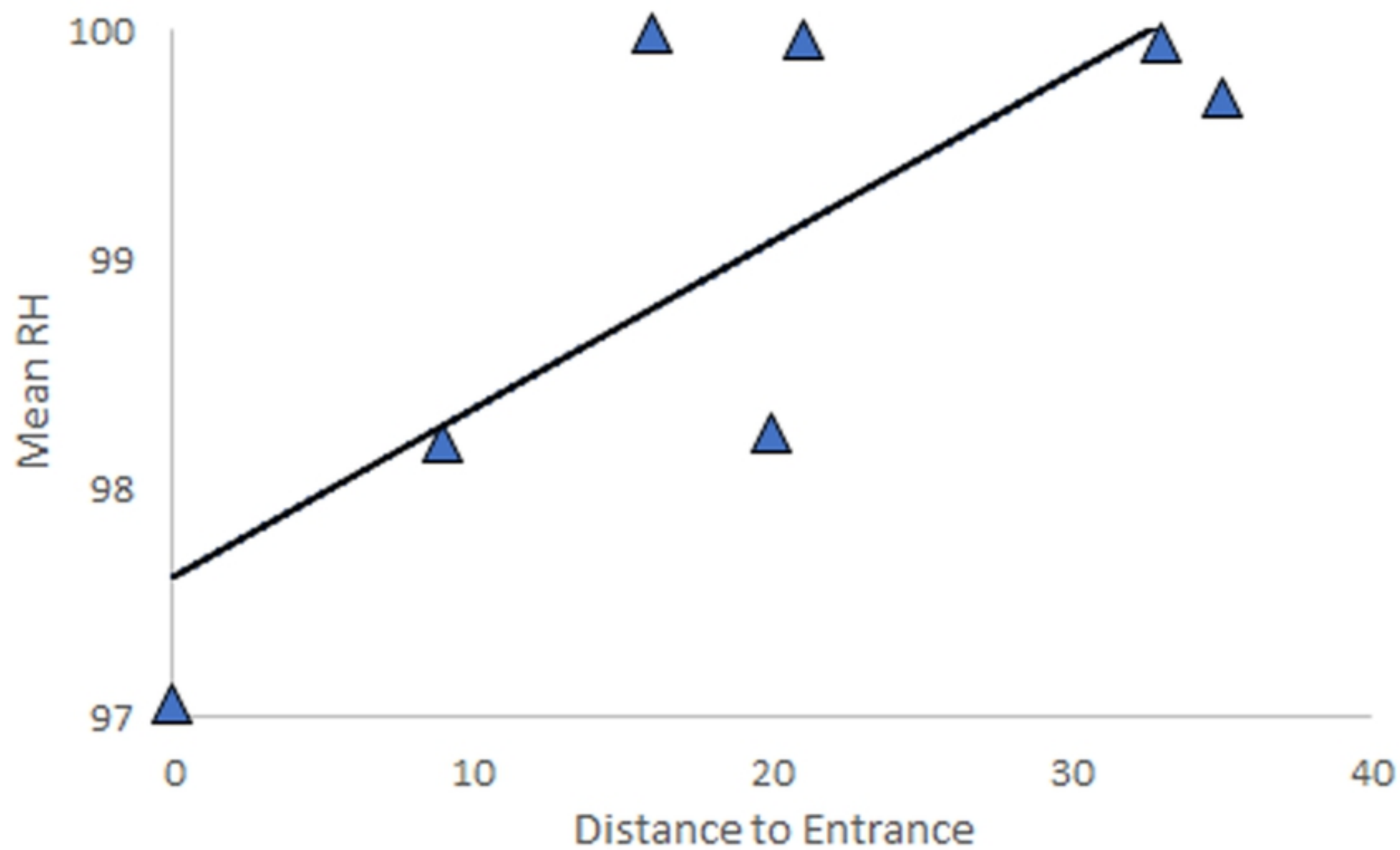
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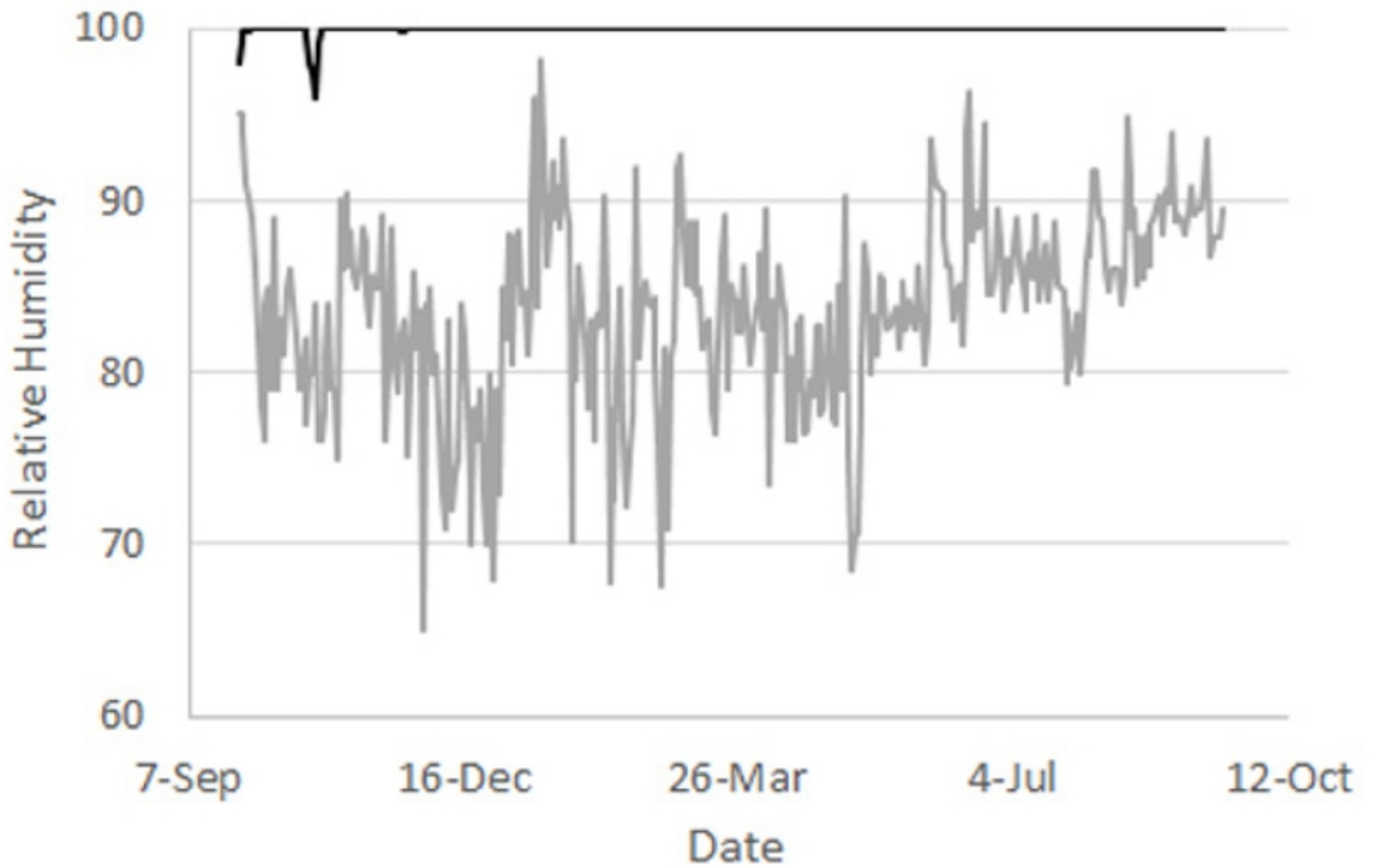
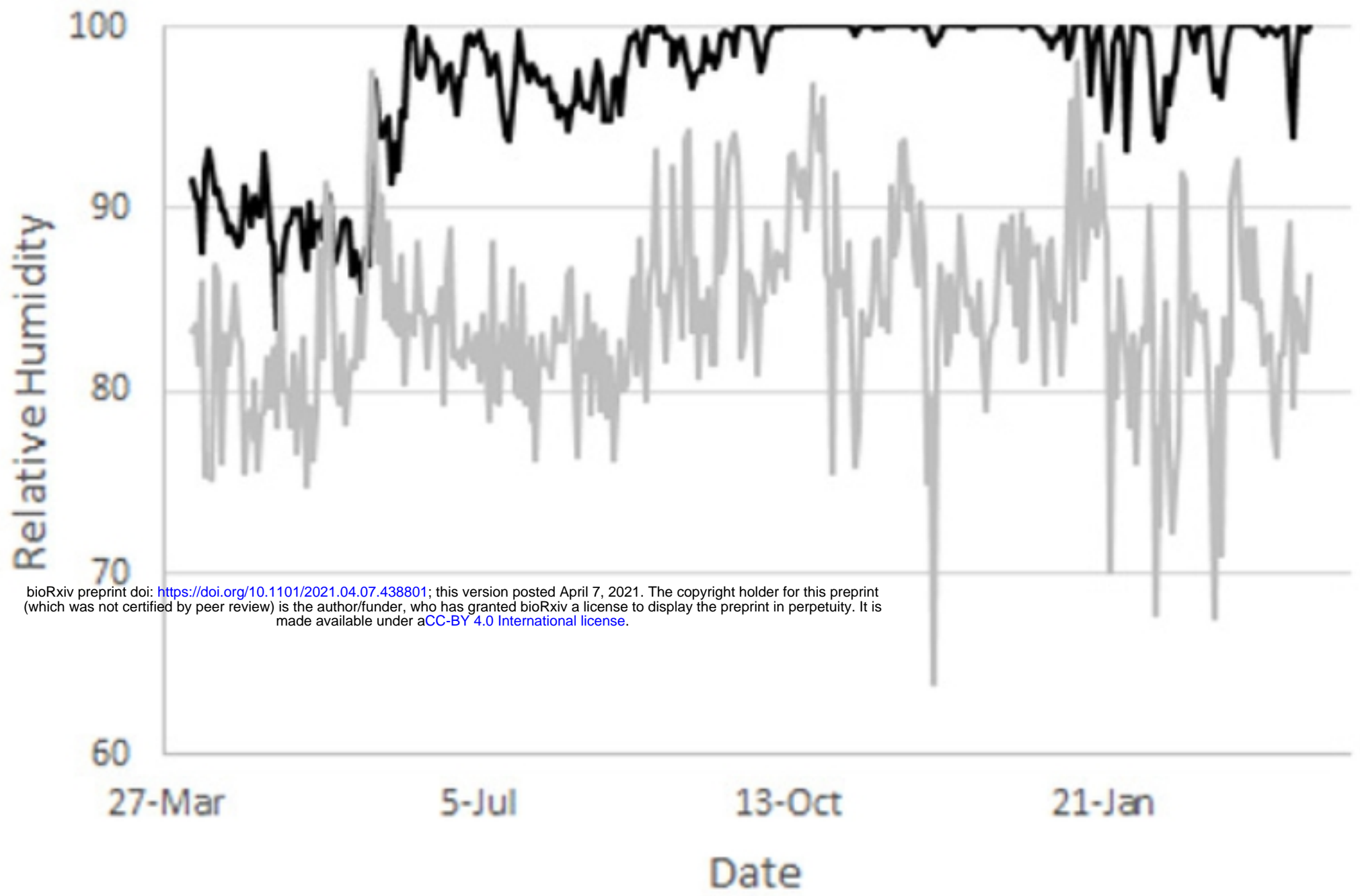
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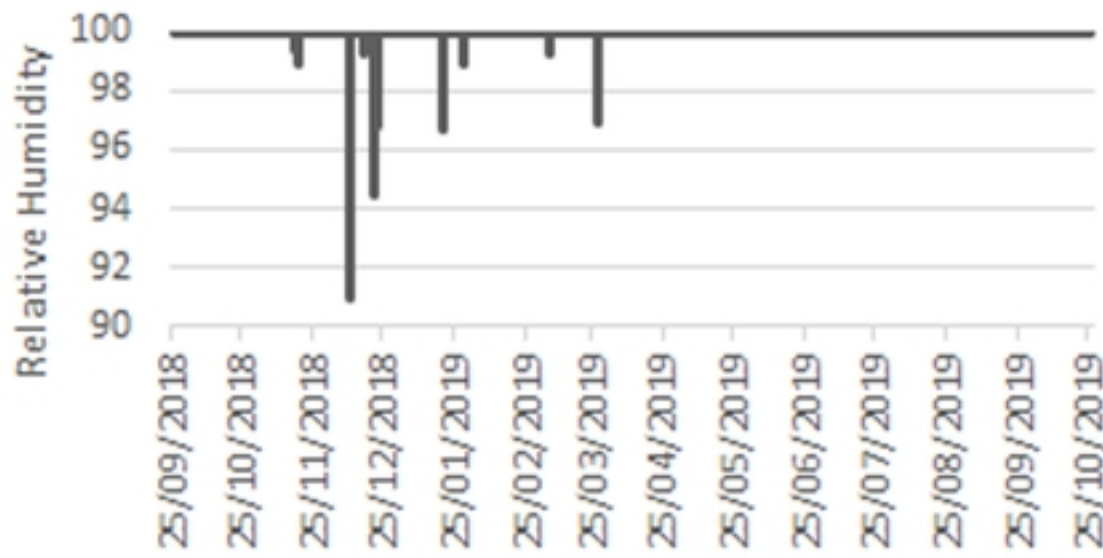


Sistema Pool Tunich
Playa del Carmen, Quintana Roo

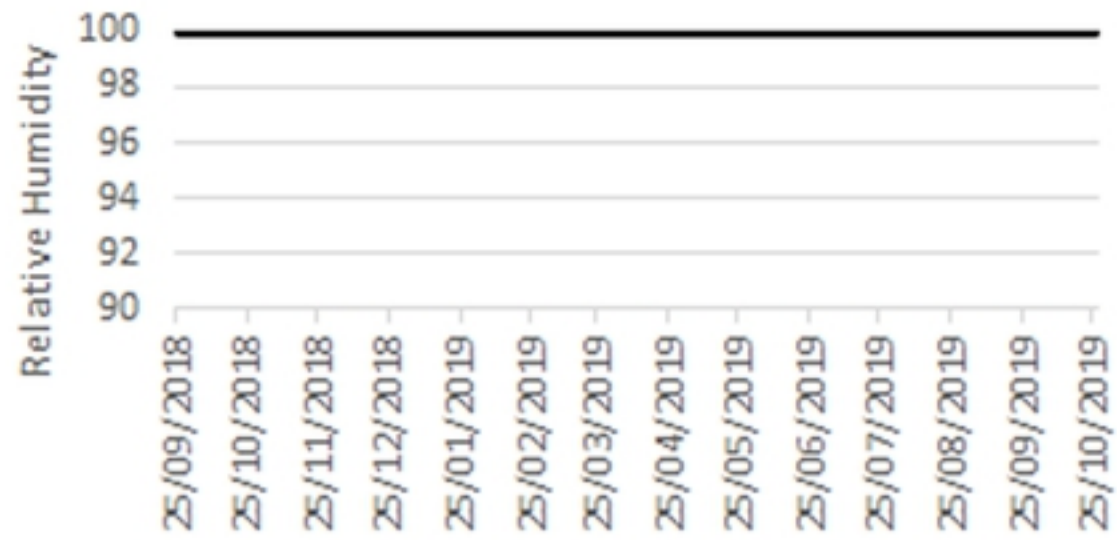




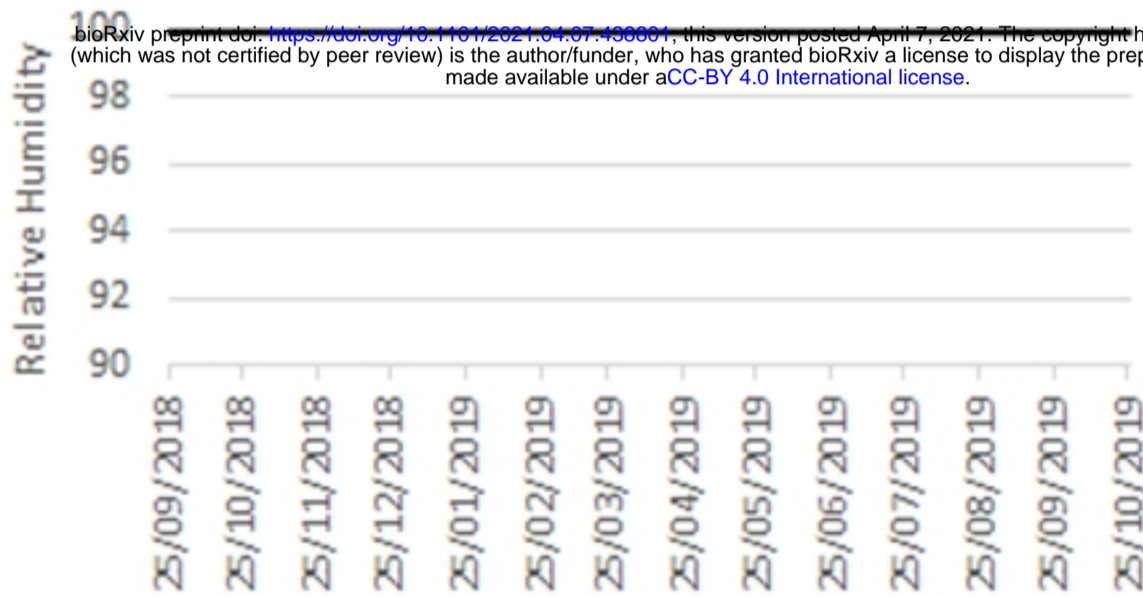
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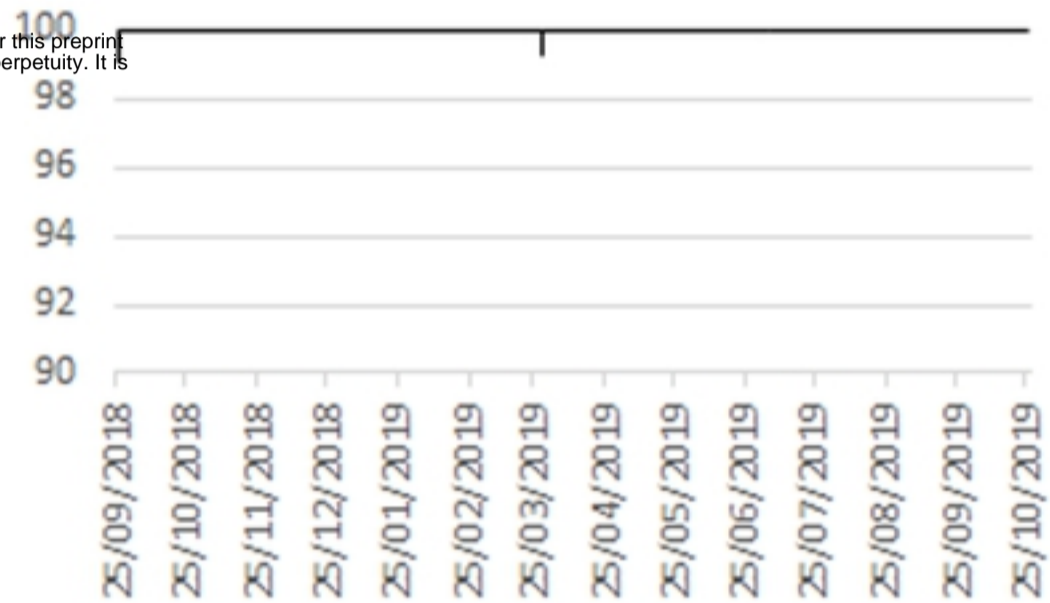
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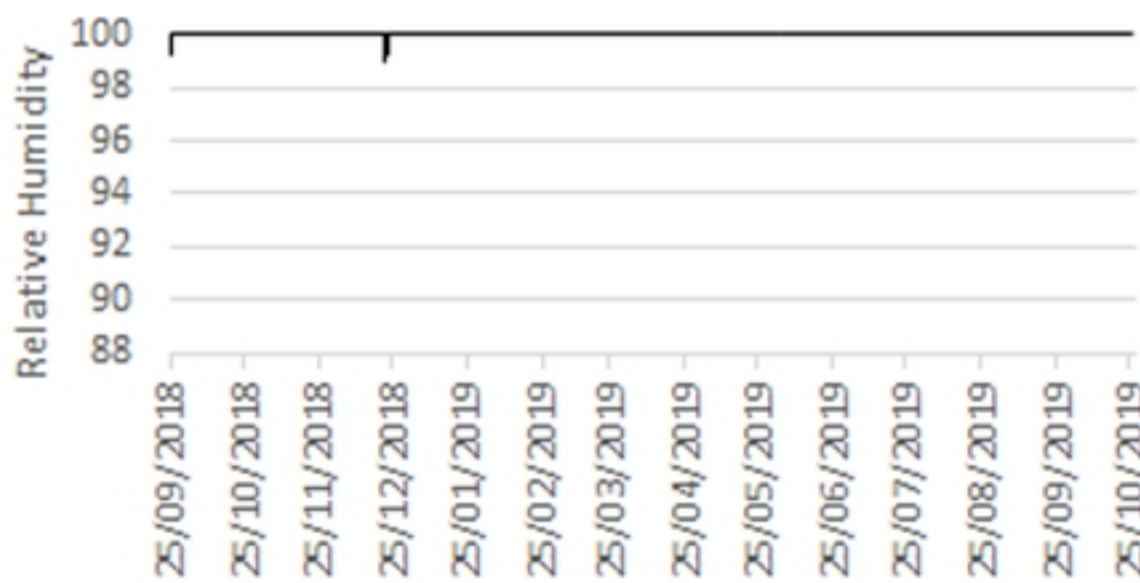
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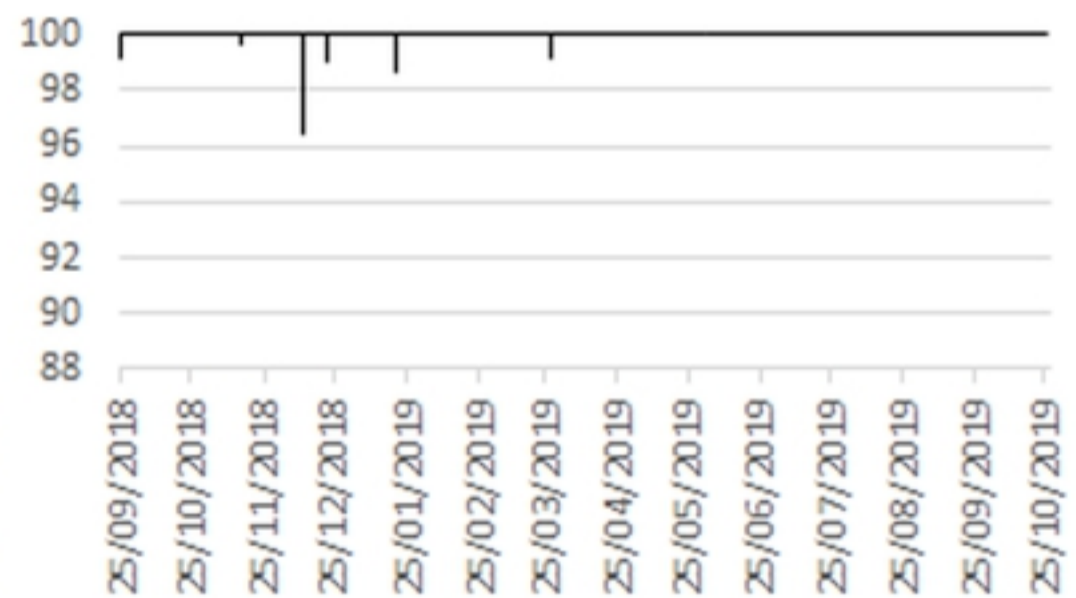
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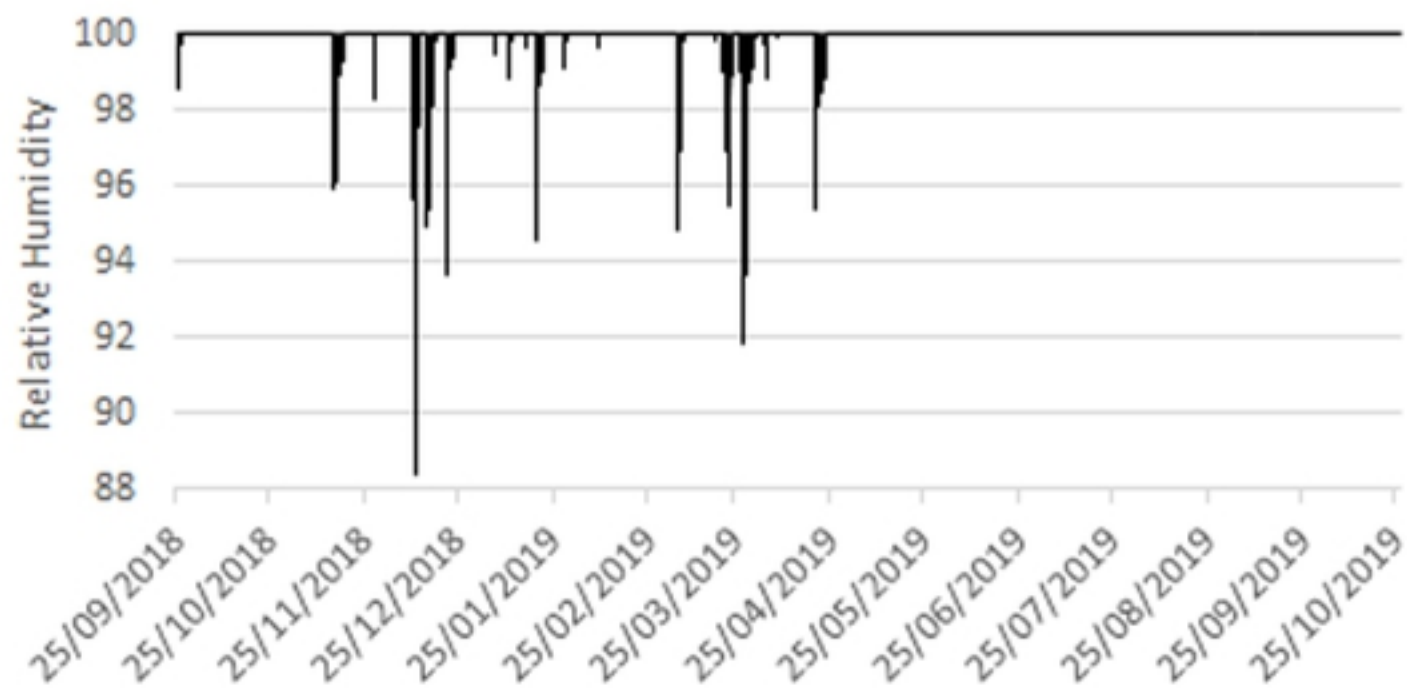
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Tuch 6

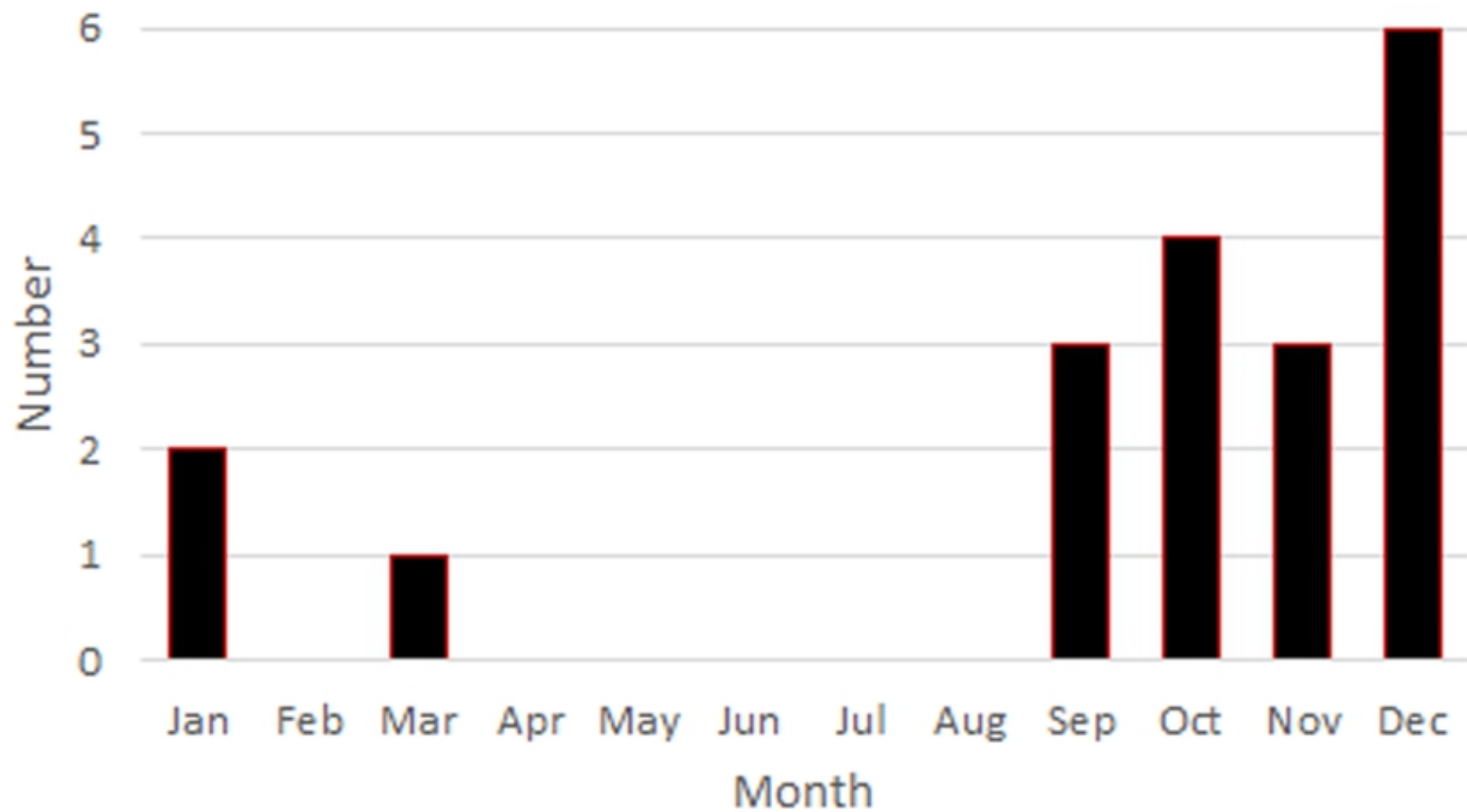


Tuch 7



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Río Secreto (Tuch)



Muévelo Rico 1



Muévelo Rico 2



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Muévelo Rico 5



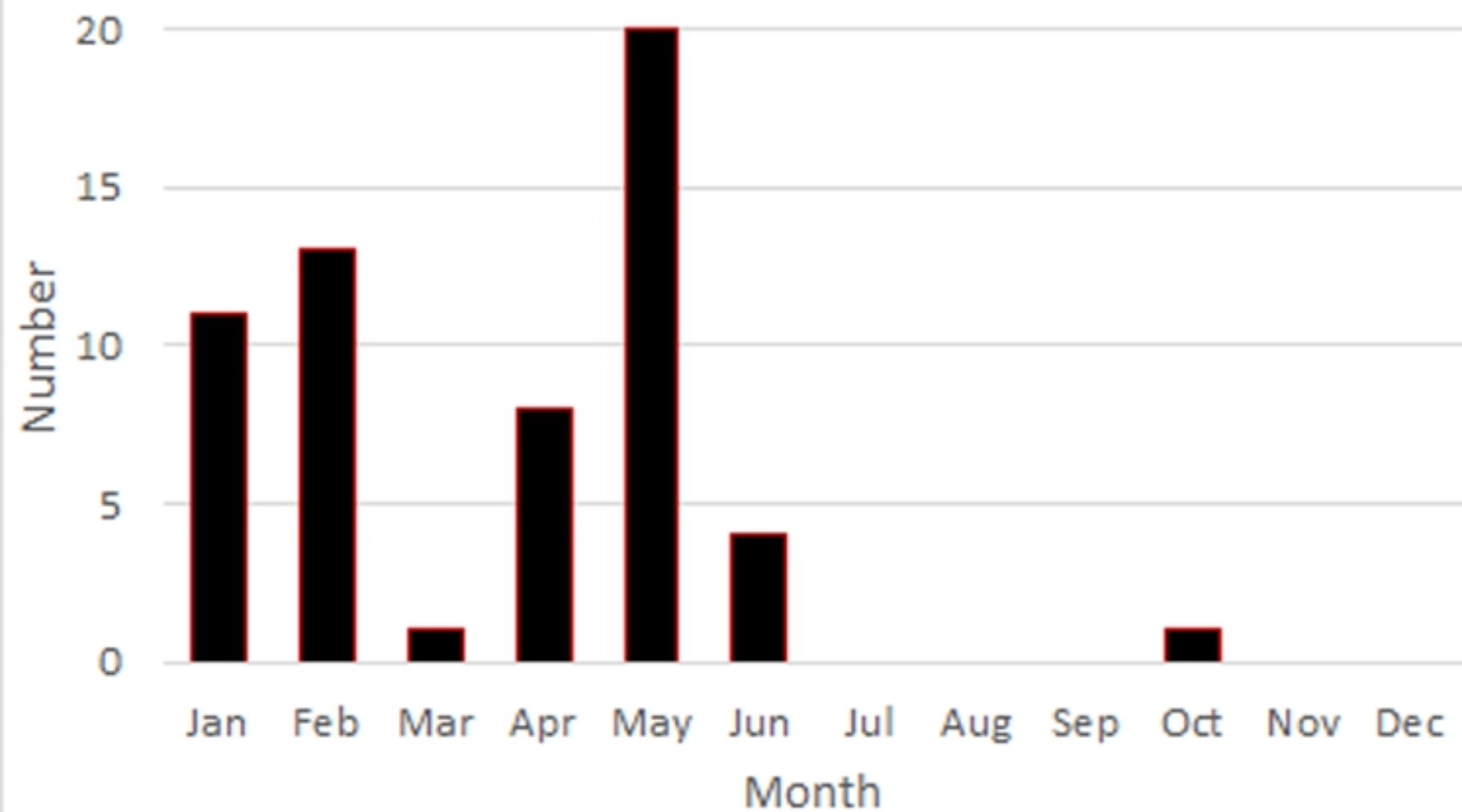
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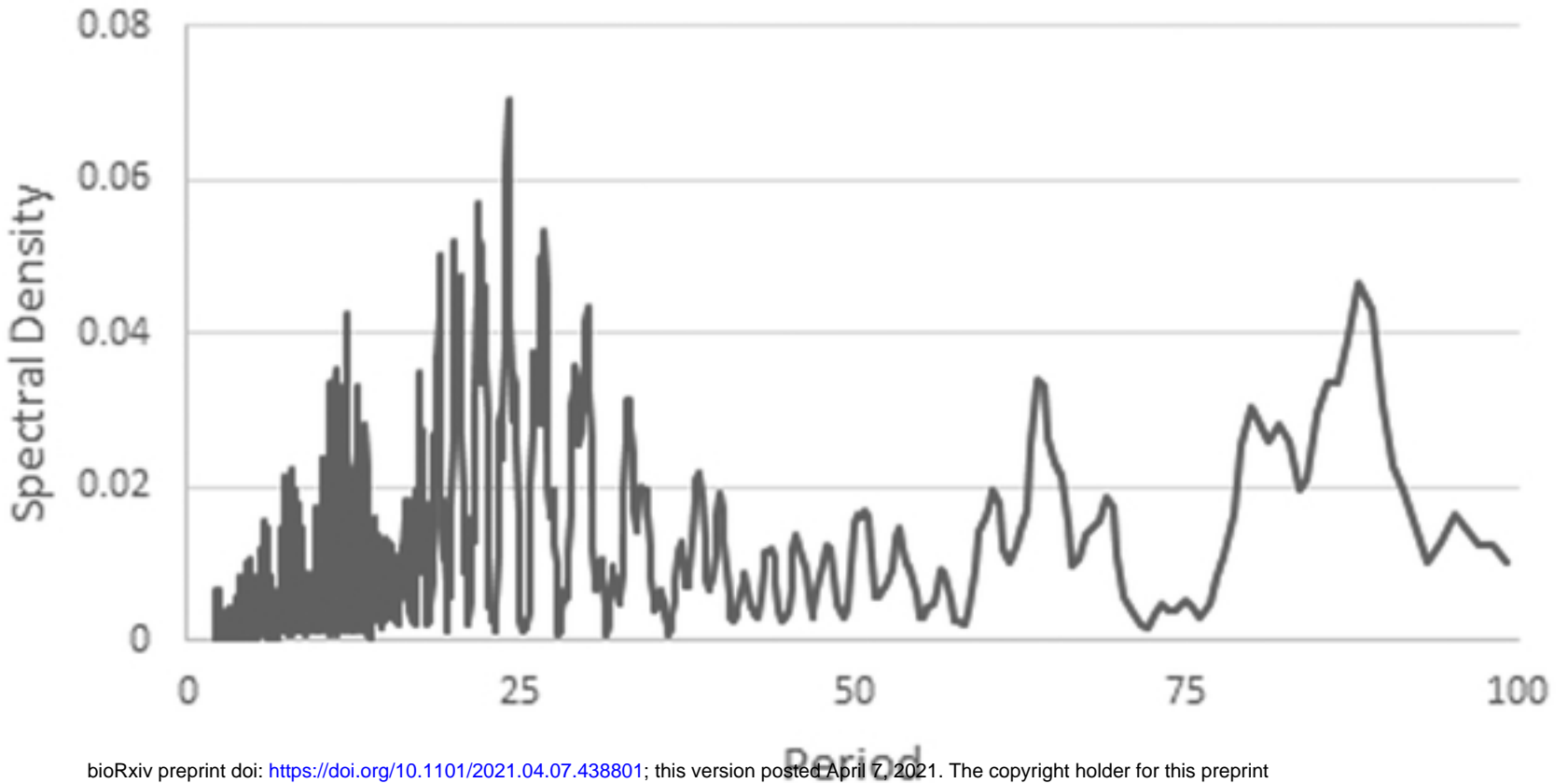
Muévelo Rico 7



Sistema Muévelo Rico 3,6,7

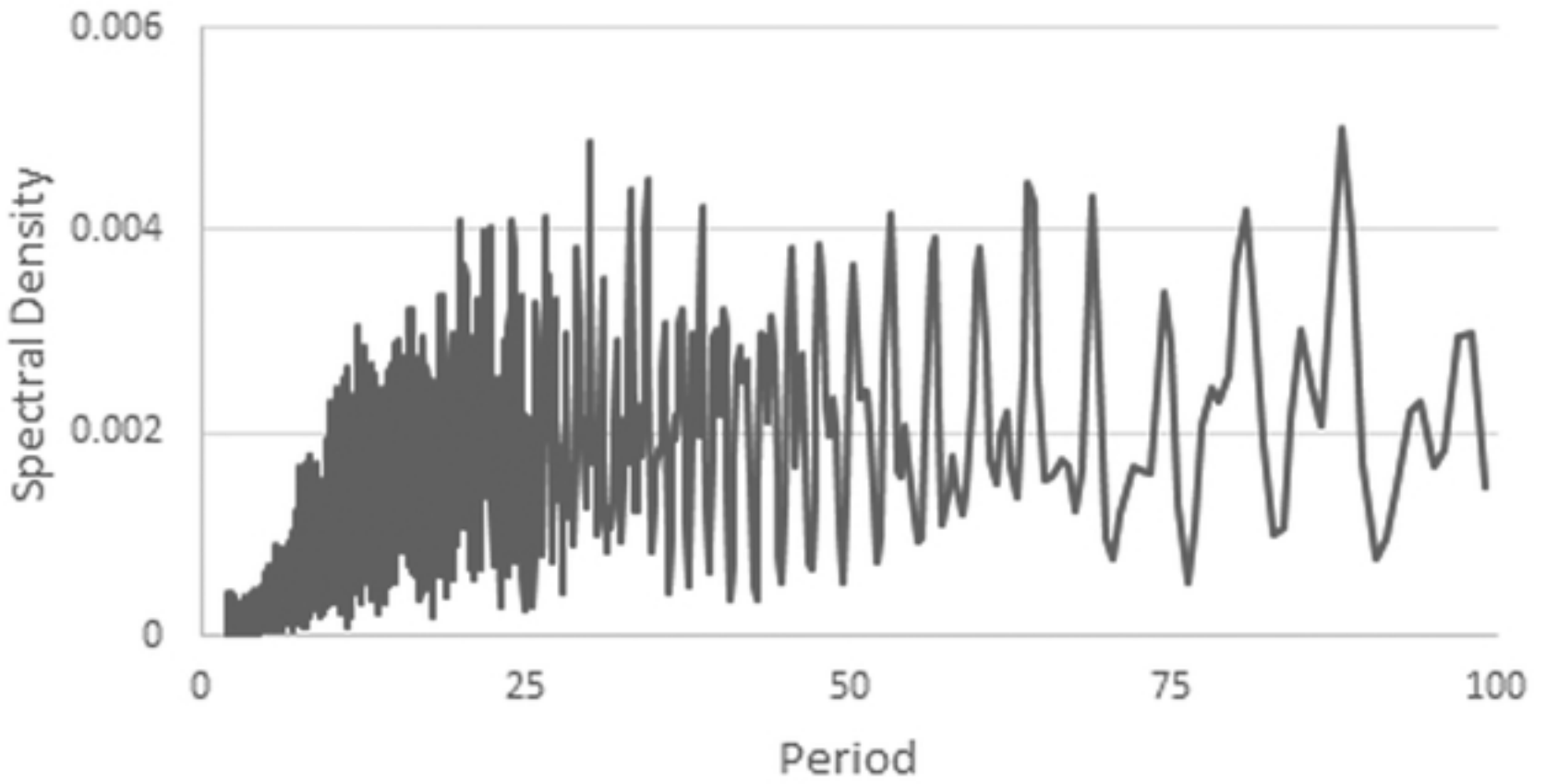


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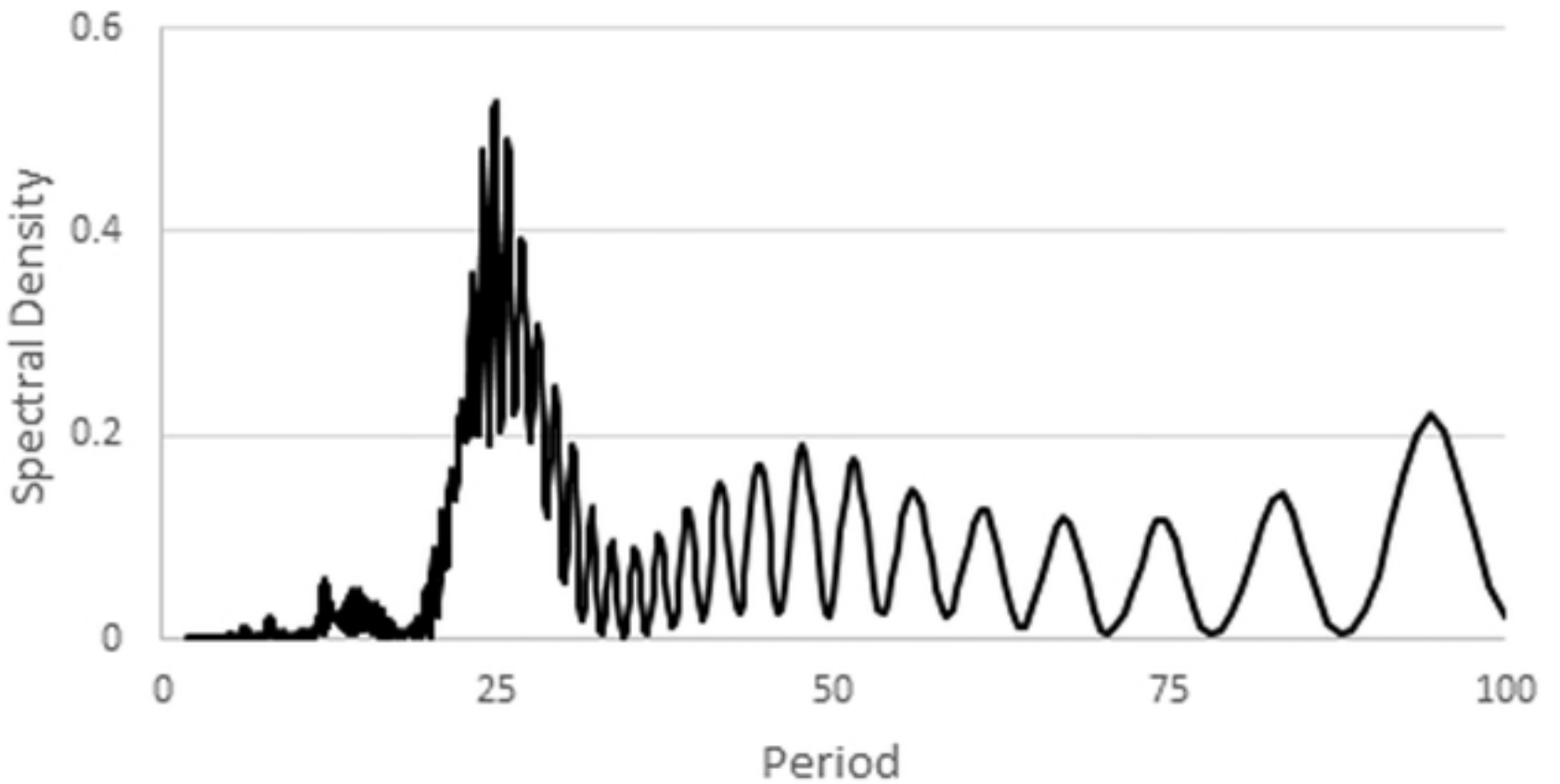


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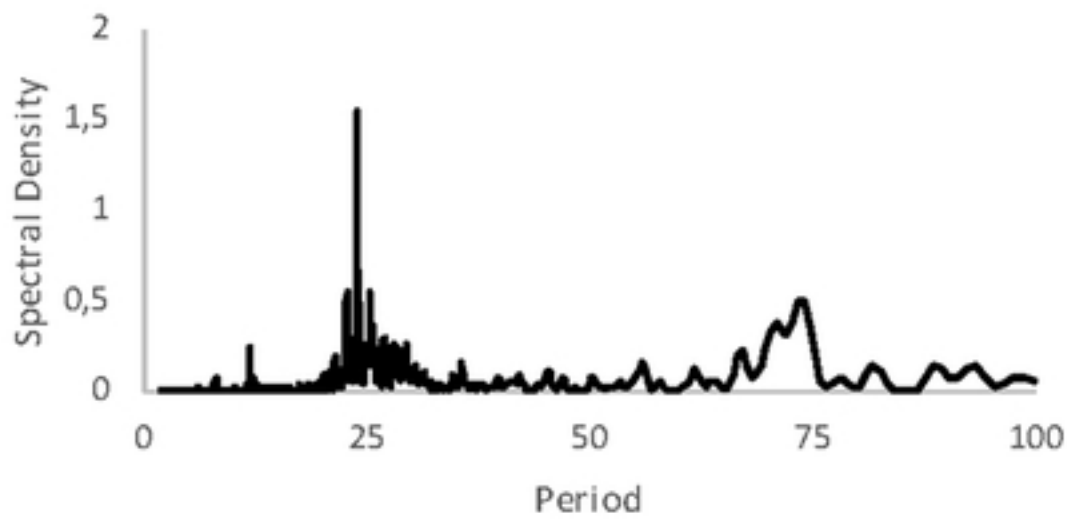
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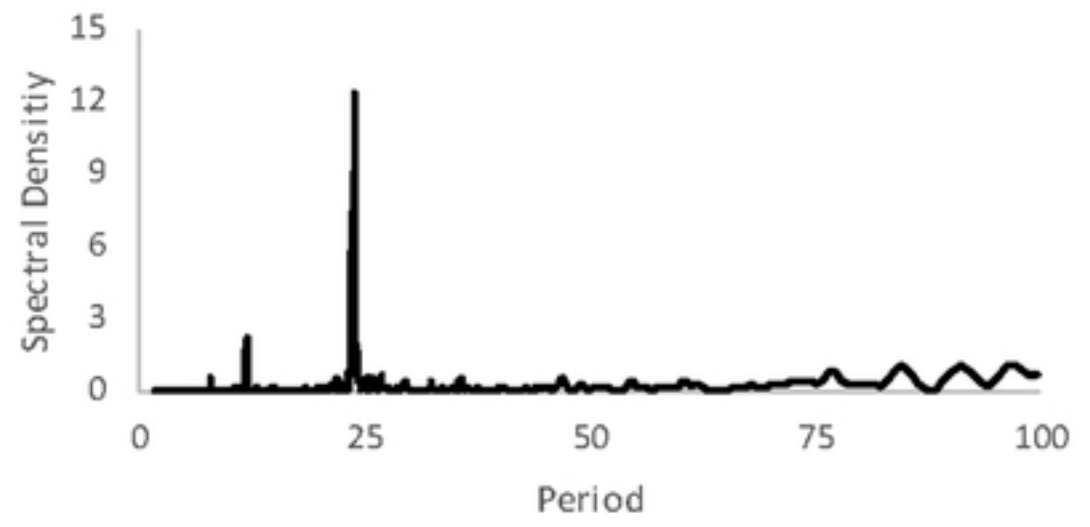
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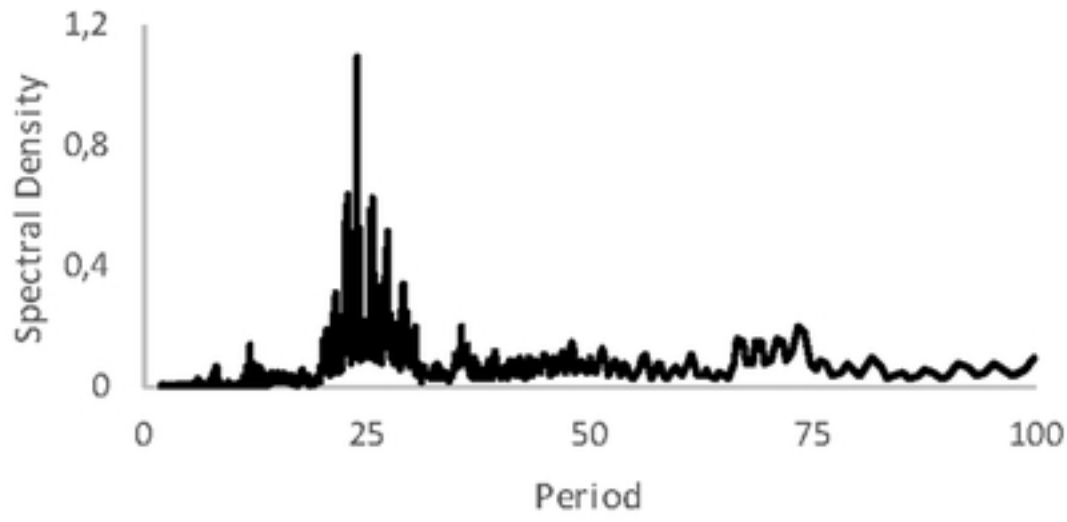


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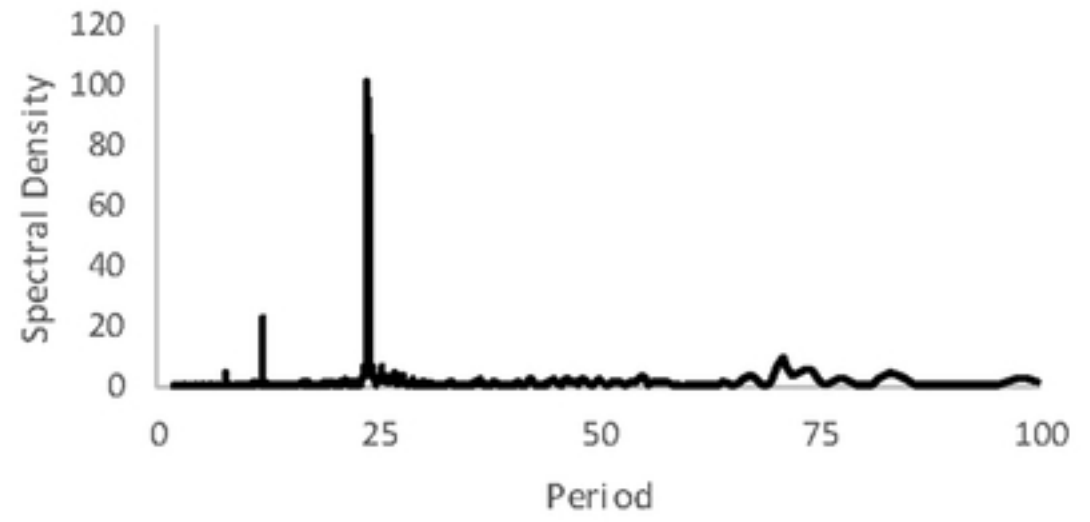


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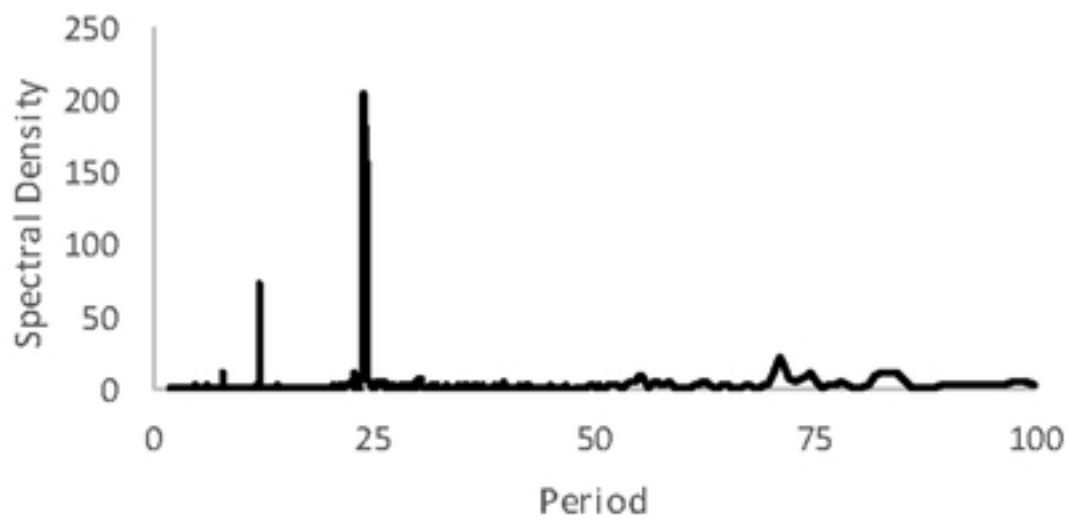
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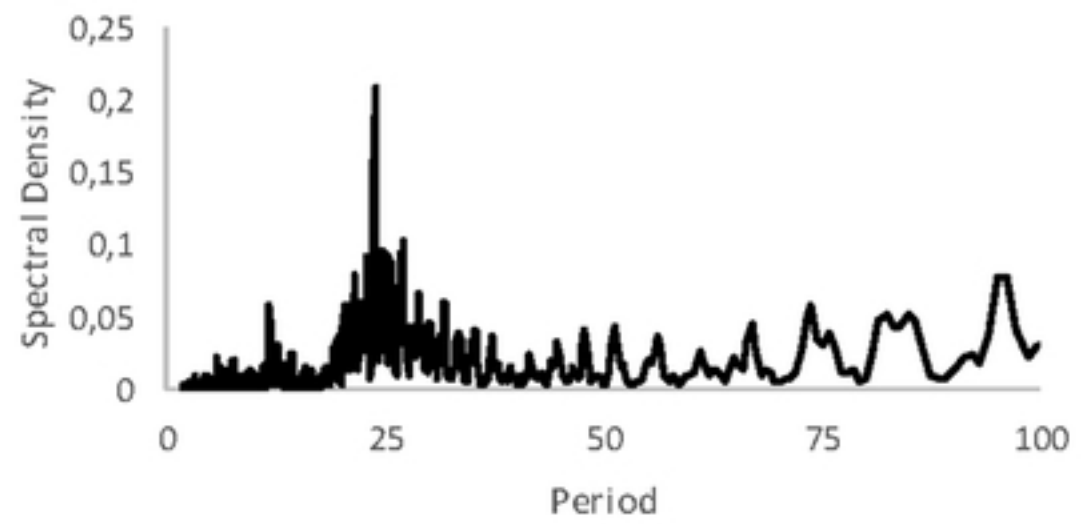
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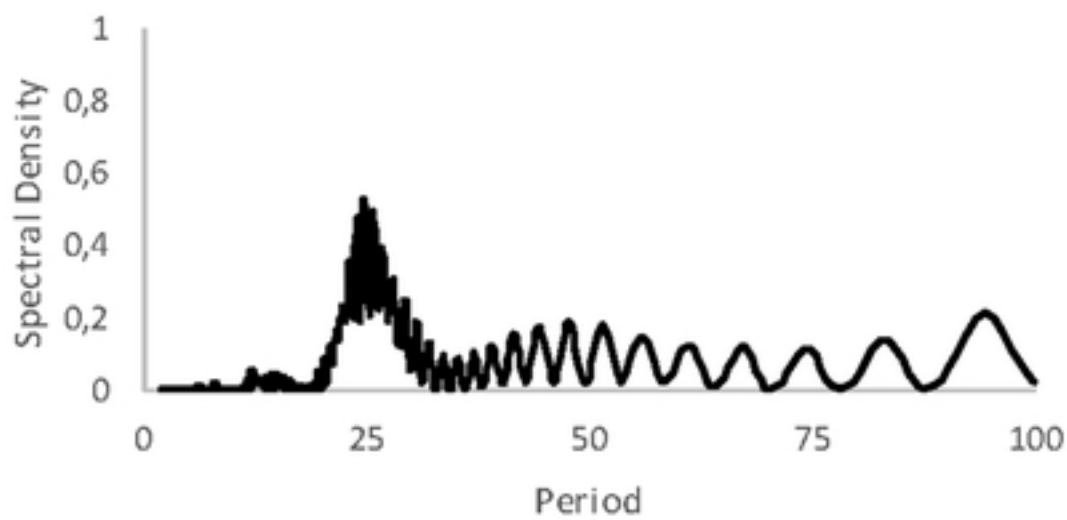
Station 5



Station 6



Station 7



Figure