Influence of rainfall on foraging behavior of a tropical seabird

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ABSTRACT

Acquiring resources for self-maintenance and reproduction is a key challenge for wild animals, and the methods that individuals employ are, in part, shaped by environmental conditions that vary in time and space. For birds, rainfall may affect behavior, impairing senses and increasing energetic costs, but its consequences on movement patterns are poorly explored. We investigated the influence of rainfall on the foraging behavior of the magnificent frigatebird, *Fregata magnificens*. This peculiar tropical seabird lacks feather waterproofing and is known to track environmental conditions while searching for food. Thus, its foraging behavior should be highly sensitive to the effects of rainfall. By GPS-tracking chick-rearing adults, we showed that frigatebirds did not avoid areas with rainfall during foraging trips, nor did rainfall influence trip characteristics. However, rainfall decreased time devoted to foraging and increased time spent perching. Moreover, it affected flight mode, inducing birds to fly slower and at lower altitudes. Wind speed, which was not correlated with rainfall, only affected behavior during night-time, with strong winds decreasing time spent perching. Our results indicate that rainfall does not affect the spatial distribution of foraging frigatebirds but does alter fine-scale foraging behavior by reducing flight activity. We suggest that the ongoing environmental change in this region, including an increase of rainfall events, has the potential to impair foraging and negatively affect fitness.

Running title: Rainfall alters foraging activity in a tropical seabird

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INTRODUCTION

Wild animals must overcome a range of challenges to maximize their fitness. Locating ample food is one such challenge, essential not only for survival but also for successfully rearing offspring, evading predators and migrating (Kramer 2001). The search for food can favour cooperation between individuals (Dumke et al. 2018), such as social information exchange (Hasenjager et al. 2020), potentially leading to drastic changes in species' ecology (Lancaster et al. 2000). Acquiring ample resources is however hindered by several factors, including inter- and intra-specific interactions (e.g. competition and predation: Ashmole 1963; Krebs 1980), physiological constraints, prior experience (Smith and Metcalfe 1994; Aubret et al. 2015), luck (Wilson et al. 2018) and environmental conditions. The latter include climatic and atmospheric components, which can act indirectly on foraging by affecting trophic interactions, influencing food webs and potentially driving long-term change in communities (Zhang et al. 2007; Bogdziewicz et al. 2020). Moreover, environmental conditions can alter foraging behavior more directly, promoting or disrupting foraging activities at fine spatial and temporal scales, by affecting the timing of feeding (e.g. ground air temperature: Kasper et al. 2008) or selection of foraging areas (Sunde et al. 2014; Udyawer et al. 2015). In birds, weather conditions and landscape features are well-known drivers of foraging behavior (Duerr et al. 2015; Scacco et al. 2019; Ventura et al. 2020), with a growing number of studies demonstrating flexibly in the tactics employed by birds in response to a varying external environment (Clay et al. 2019; Cecere et al. 2020; De Pascalis et al. 2020).

Rainfall is a key weather component, known to affect avian activity and movement patterns (Elkins 2010). Wet plumage can result in severe heat loss

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74   (Stalmaster and Gessaman 1984; Wilson et al. 2004), impair locomotor performance

75   and flight capabilities, and increase body mass and consequently wing loading

76   (Mahoney 1984; Ortega-Jiménez et al. 2010; Ortega-Jimenez and Dudley 2012a), all

77   conditions that are expected to increase energy expenditure (Hertel and Ballance 1999).

78   In addition to direct effects on energy expenditure, rainfall has the potential to impair

79   vision and hearing, reducing the perceptive accuracy of the surrounding environment

80   (Yorzinski 2020). Overall, rain can reduce foraging efficiency in several ways, for

81   example by impairing the localization of prey, inhibiting detection of predators and thus

82   increasing the need for vigilance, or inducing shifts in preferred foraging areas (Hilton

83   et al. 1999; Sergio 2003; Whittingham et al. 2004; Fernández-Juricic 2012).

84   Despite its potential to disrupt foraging and alter time-activity budgets, the

85   behavioral strategies that birds have evolved to cope with rainfall are poorly

86   investigated. Avoidance of rain by sheltering has been documented (e.g. Cauchard and

87   Borderie 2016; Wilkinson, et al. 2019), especially in the tropics where intense but

88   transient downpours can take place (Elkins 2010). If sheltering is not possible due to

89   habitat and/or body size (e.g. large raptors), individuals can remain perched to minimise

90   exposure to rain (Elkins 2010). Relocating to more distant areas, to avoid strong rain

91   and wind, has been observed in some species prior to the arrival of perturbation fronts,

92   as birds are believed to be capable of sensing - to some extent - the arrival of storms

93   (Blomqvist and Peterz 1984; Streby et al. 2015; Weimerskirch and Prudor 2019).

94   Finally, some species have evolved morphological or behavioral adaptations to cope

95   with rainfall. For example, birds with high feeding rates such as hummingbirds can

96   actively fly and forage in the rain, using both aerial and perched shaking techniques to

97   expel water from their plumage (Ortega-Jimenez and Dudley 2012b). While most of the

98   existing studies provide anecdotal evidence for behavioral responses to rainfall, or

99   performed investigations at the foraging trip level (Pistorius et al. 2015; Lane et al.

100   2019), a fine-scale understanding of the influence of rain on foraging behavior,

101   particularly during energy-demanding periods of the life cycle such as chick-rearing, is

102   currently lacking.

103   Frigatebirds are intriguing candidate species to investigate the effect of rainfall

104   on foraging, given their ecology and life-history traits. They are large-bodied marine

105   predators (1-1.9 kg; Diamond and Schreiber 2002) widely distributed across the tropics,

106   an area that experiences fluctuating and sometimes heavy rates of rainfall (Mandeep et

107   al. 2011). Owing to their unusual morphological characteristics (limited feather

108   waterproofing and partially webbed feet), frigatebirds are obligate opportunistic surface

109   feeders that rely heavily on visual cues to detect prey (Diamond and Schreiber 2002).

110   They are highly efficient flyers due to their low wing loading (Weimerskirch et al.

111   2004) and are thus capable of ranging over large distances to search for food

112   (Weimerskirch et al. 2016; Austin et al. 2019). Furthermore, they are known to track

113   environmental components such as frontal regions and transport fronts to increase

114   foraging opportunities (Tew-Kai et al. 2009; De Monte et al. 2012) and may be one of

115   the few bird species able to ride out a storm (Cramp and Simmons 1977). While

116   provisioning offspring, frigatebirds act as central-place foragers, implying that they

117   have spatial and temporal constraints on their movements (Orians and Pearson 1979).

118   To meet the high energetic demands associated with this phase of the life cycle,

119   frigatebirds are expected to adjust foraging behavior to maximise efficiency in the

120   spatio-temporally variable environments that they inhabit (Weimerskirch et al. 2003a;

121   De Monte et al. 2012). However, their functional traits may render them particularly

122   susceptible to foraging disruption caused by rainfall.

123   In this study, we investigated whether rainfall alters the foraging behavior of

124   chick-rearing magnificent frigatebirds (*Fregata magnificens*, hereafter referred to as

125   'frigatebirds'). Assuming that searching for food under rainy conditions results in

126   increased energy expenditure, and given that frigatebirds show some capability to

127   anticipate the arrival of perturbation fronts (Weimerskirch and Prudor 2019), we

128   hypothesise that chick-rearing frigatebirds should: 1) avoid foraging in areas subjected

129   to heavy rainfall; and 2) modify their at-sea behavior when encountering rain. The latter

130   could be achieved by a) increasing flight height above the rainy cloud front and

131   avoiding rainfall (frigatebirds are capable of flying at very high altitudes;

132   (Weimerskirch et al. 2003b) or b) reducing activity until the unfavourable conditions

133   pass. Rainfall events can be associated with light-to-strong changes in wind intensity,

134   since clouds form in frontal depression systems where air masses move (Ahrens 2011).

135   Thus, to account for confounding effects of wind speed on fine-scale behavioral

136   responses to rain, we included wind speed in our analysis.

137

138   **MATERIALS AND METHODS**

139   **Animal capture, handling and data preparation**

140   During the main chick-rearing periods (February to May) in 2017 and 2019, 44 (2017: *n*

141   = 22; 2019: *n* = 22) breeding adults were equipped with solar-powered GPS-GSM

142   biologgers (Movetech Telemetry) at a colony on Little Cayman, Cayman Islands, in the

143   Central Caribbean (19° 39.8'N, 80° 4.9'W). Individuals were caught on the nest with a

noose-pole, and devices were attached to a small number of contour feathers on the back using waterproof tape (mean ± SD handling duration: 15 ± 3 min). In all cases, birds were observed returning to attend the chick shortly after release. Owing to difficulties in recapturing birds after first capture, loggers were not retrieved and were assumed to have been shed when transmissions ceased. Devices were set to record positions on three dimensions (latitude, longitude and altitude) every 15 mins. Device mass ranged between 23.2 and 25.8 g, and relative device load (including attachment) was 2.9 ± 0.4 % (mean ± SD) of body mass. To assess the potential impact of handling and device attachment, we recorded breeding success (proportion of nests that fledged a chick) of all experimental nests and a group of unhandled control nests. No significant difference in fledging success of experimental and control nests was observed (2017: Austin et al. 2019; 2019: control, $n = 99$, fledging success = 0.63; experimental, $n = 22$, fledging success = 0.45, Fisher's exact test, $P = 0.16$, odds ratio = 0.50, power = 0.27). Fieldwork was performed under permissions of the Department of Environment, Cayman Islands Government and National Trust of the Cayman Islands.

Foraging trips were identified as movements ≥1 km from the colony, lasting ≥ 30 min (Austin et al. 2019). Incomplete trips and very short trips (≤ 2-3 locations; $n = 33$), likely to represent colony-based movements inside the reef, were also removed from further analyses. Only foraging trips undertaken when the tracked bird was actively rearing a chick were retained. For birds that lost their chick during the tracking period, we only included trips performed before the last date the chick was recorded alive. Duplicate and unrealistic locations based on derived ground speed, were identified and removed using the 'SDLfilter' R package (Shimada 2019). Overall, we obtained information on 517 complete foraging trips from 33 birds (15 males and 18

168 females; mean ± SD; trip duration: 30 ± 43 hours; foraging trips per individual: 16 ± 35;

169 Fig. 1). The tracking period spanned March to late May in 2017 (*n* = 14 individuals) and

170 March to late October in 2019 (*n* = 19 individuals). GPS locations were matched to

171 gridded environmental data (cell size: 0.25° × 0.25°; ~ 27 km × 27 km, temporal

172 resolution: 1 h). Precipitation data (mm/h, a measure of rainfall), and both U and V

173 wind component data, from the ERA5 dataset (Hersbach et al. 2020) were downloaded

174 from the Copernicus Climate Change Service

175 (https://cds.climate.copernicus.eu/cdsapp#!/home). Wind speed (m/s) was then derived

176 from U and V wind components using the "rWind" R package (Fernández-López and

177 Schliep 2019).

178

179 **Statistical analyses**

180 *Effect of rainfall on spatial distribution* - A Resource Selection Function (RSF)

181 approach was used to investigate whether frigatebirds avoided areas with high rainfall

182 during foraging trips. Environmental features at locations visited by the animal (i.e.

183 'used locations') were compared to the features at a set of random locations drawn from

184 an area assumed to be available to the animal (i.e. 'available locations') (Muff et al.

185 2020). Defining an availability domain for frigatebirds is challenging, since they are

186 long-distance foragers that exploit a wide range of environments, including pelagic

187 waters, coasts, islands and inland areas (see Austin et al. 2019). Therefore, to achieve

188 the highest possible ecological realism, we generated two sets of random locations by

189 rotating each foraging trip (anchored at its initial location, i.e. the colony site) by a

190 randomly selected angle (Freeman et al. 2010; Cecere et al. 2018). For each real trip, we

191   calculated the proportion of locations falling on land, and then constrained each rotated

192   trip to have a similar number of locations on land (± 10%). If the original trip had less

193   than 10% of locations on land, we allowed the rotated trip to fall entirely over sea. If the

194   above conditions were not met after 1000 iterations of random rotations, the trip was

195   discarded ($n = 46$). This approach allowed us to work on raw presence data, and

196   prevented biases being introduced by any unrealistic overlap with - or absence of - land.

197   We generated two rotated trips for each real trip, confirming that these were different to

198   each other by visual inspection. For both the real and simulated trips, the time of each

199   location was rounded to the nearest hour, and the most central location in each hourly

200   time bin was retained with all others discarded. This method was followed to avoid

201   excessive temporal autocorrelation between subsequent consecutive locations and to

202   ensure that the temporal resolution of rainfall data matched that of the GPS data.

203   Overall, the dataset used for the RSF analysis contained 13330 used (471 trips

204   from 33 individuals) and 26660 available (942 trips from 33 individuals) locations (see

205   Supporting information). To investigate the effect of rainfall on the spatial distribution

206   of frigatebirds, we fitted a weighted logistic regression model to the data, modelling the

207   probability of having a used vs. available location in relation to rainfall, and including a

208   by-individual random intercept and slope. The model was fitted with the *glmmTMB*

209   function in the "glmmTMB" R package (Magnusson et al. 2020), using the

210   parametrization recommended by Muff et al. (2020) for RSFs.

211   *Effect of rainfall on foraging trip characteristics* – To assess the broad-scale effect of

212   rainfall on foraging behavior, we calculated the following characteristics for each

213   foraging trip: trip duration (h), mean distance from colony (km), maximum distance

214   from colony (km) and total distance travelled (km). We then fitted GLMMs using the

215 "lme4" R package (Bates et al. 2015), with each trip characteristic as the response

216 variable, and mean rainfall experienced during each foraging trip as an explanatory

217 variable. Bird identity was included as a random intercept, and significance was

218 assessed using likelihood ratio tests. After visual inspection of frequency distributions,

219 we fitted a Gamma error distribution with a log-link function. Model assumptions were

220 checked using the "performance" R package (Lüdecke et al. 2020).

221 *Effect of rainfall and other environmental variables on behaviors* - Generalized Hidden

222 Markov Models (HMMs) were used to test the effect of two environmental variables

223 associated with perturbation fronts and potentially affecting foraging behavior of

224 frigatebirds (i.e. rainfall and wind speed) using the "momentuHMM" R package

225 (McClintock and Michelot 2018). As HMMs require regular time steps, we linearly

226 interpolated and re-sampled the dataset at 15-min intervals, using the "adehabitatLT" R

227 package (Calenge 2006). To each interpolated location, we then assigned the closest

228 matching real-time altitude, rainfall and wind speed values. Since frigatebirds are highly

229 visual predators, and considering that they can spend a prolonged time aloft (up to 2.1

230 months, Weimerskirch et al. 2016), it is likely that circadian rhythms and ambient light

231 could influence their behavioral responses to weather variability. Therefore, we

232 determined if each location occurred during daytime (coded 1) or night-time (coded 0),

233 using the *crepuscule* function (astronomical twilight) from the R package 'maptools'

234 (Bivand and Lewin-Koh 2018). A three-state multivariate HMM was run using the

235 Viterbi algorithm to estimate the most likely behavioral state sequence (Zucchini et al.

236 2017). The number of states was chosen based on *a priori* knowledge of frigatebird

237 behavior (Austin et al. 2019). Initial parameter priors used in the model were chosen

238   after comparing negative log-likelihood values of several candidate models ($n = 20$), run

239   iteratively using a range of randomly selected reasonable prior values.

240   Data streams used in the model were step length (i.e. distance travelled), turning

241   angle (i.e. change of movement direction) and altitude (i.e. meters above sea level).

242   Despite GPS-derived altitude being less accurate when compared to latitude and

243   longitude, it can be reliably used in HMMs (Clark et al. 2019). A Gamma distribution

244   was used to model step length and altitude, while a Von Mises distribution was used to

245   model turning angle, and a zero-mass parameter was applied to step length to account

246   for zero inflation. We modelled the transition probabilities as a function of

247   daytime/night-time, rainfall and wind speed. The two latter variables were very weakly

248   correlated ($r = 0.03$), hence our results were unaffected by collinearity. To test the

249   relative influence of environmental variables (as well as their combined effect) on

250   model performance, a set of ecologically meaningful candidate models were compared.

251   Starting from a null model, we sequentially added each covariate, as well as their two-

252   way interaction, and used AIC to select the most parsimonious model. To assess how

253   environmental covariates affected the proportion of time spent in each behavior, we

254   calculated and plotted the stationary-state probabilities (representing the equilibrium of

255   the process) for each covariate. When plotting rainfall, wind speed was kept at its mean

256   value (5.11 m/s). When plotting wind speed, rainfall was kept at its mean value (0.09

257   mm/h). When plotting daytime/night-time, both rainfall and wind speed were kept at

258   their mean values. Finally, for each covariate we extracted the predicted stationary

259   probability (with 95% CI) for the minimum and maximum actual values recorded

260   (rainfall: 0 and 6 mm/h; wind speed: 0 and 13 m/s) during both daytime and night-time.

261   To assess the effect of covariates on state transition probabilities, we plotted transition

262   probabilities as a function of each covariate (keeping the other at its mean value) during

263   both daytime and night-time, and extracted the transition probability (with 95% CI) on

264   the real (i.e. natural) scale for the maximum and minimum values recorded. All analyses

265   were undertaken using R software version 3.5.1 (R Core Team 2018).

266   ## RESULTS

267   **Effect of rainfall on spatial distribution and trip characteristics**

268   Frigatebirds encountered rainfall events (>0.005 mm/h) during the majority of foraging

269   trips (94 %, Fig. 2). The mean number of hourly intervals with rain per trip was 17 ± 23

270   SD (56.6 % of the mean trip duration). Overall, used locations were similarly rainy

271   (0.085 mm/h $\pm$ 0.002 SE) as available ones (0.084 mm/h $\pm$ 0.002 SE). At the population

272   level, frigatebirds were not significantly more likely to occur in less rainy locations

273   (weighted logistic regression analysis; $\hat{\beta} = -0.026 \pm -0.06$ SE, P = 0.68). At the

274   individual level, frigatebirds were rather homogeneous in their lack of a spatial response

275   to rainfall (random slope effect: $\sigma^2 = 0.08 \pm 0.29$ SD). The spatial distribution of

276   foraging frigatebirds was thus largely independent of rainfall.

277   There was no significant effect of rainfall on foraging trip characteristics (trip

278   duration: estimate = 0.60 $\pm$ 0.03 SE, $\chi^2 = 3.5$, df = 1, P = 0.06; mean distance from

279   colony: estimate= -0.10 $\pm$ 0.20 SE, $\chi^2 = 0.1$, df = 1, P = 0.70; total distance travelled:

280   estimate = 0.10 $\pm$ 0.30 SE, $\chi^2 = 0.1$, df = 1, P = 0.80; maximum distance from colony:

281   estimate = -0.10 $\pm$ 0.20 SE, $\chi^2 = 0.2$, df = 1, P = 0.70).

282

283   **Characterization of behaviors**

284   The fitted HMM assigned each location to one of three states, which were considered to

285   represent the following behaviors: searching/foraging (moderate step length and

286   altitude, and high turning angle); travelling (large step length, high altitude and low

287   turning angle); perching (very low step length and altitude, and high turning angles)

288   (Table 1, see also Supporting information). Locations assigned to each behavior were

289   visually inspected. The vast majority of locations classified as perching (95.7%) were

290   tightly clustered on land, while only 4.3% were interspersed within other behavioral

291   states at sea, reflecting either infrequent inaccuracies in behavioral assignment and/or

292   perching on boats or other floating objects (e.g. channel markers, buoys). We are

293   therefore confident that most perching behaviors were correctly identified by the model.

294

295   **Effect of rainfall and other environmental variables on behaviors**

296   Including environmental covariates strongly improved model fit (ΔAIC = 1042.5

297   compared to the null model). The best fitting model included all candidate

298   environmental covariates, as well as a two-way interaction between wind speed and

299   daytime/night-time (Table 2). Overall, time spent in each behavior changed according to

300   daytime/night-time, with higher probability of perching during night-time than during

301   the day (Supporting information). Changing levels of rainfall (range 0.0 - 6.9 mm/h)

302   affected the time spent in each behavior in a similar fashion during both day and night

303   (Fig. 3a,b): with increasing rainfall, perching probability increased almost to 1 while

304   travelling and foraging/searching probability decreased to near zero. During daytime,

305   the probability of being in a given behavioral state remained relatively constant as wind

306   speed increased (Fig 3c). However, during night-time (Fig 3d), the probability of

perching decreased from 0.78 (95% CI 0.71-0.84) when there was no wind (0 m/s) to

0.07 (95% CI 0.04-0.12) at high wind speeds (13 m/s). In contrast, the probabilities of

travelling and search/foraging increased with increasing wind speed: travelling

increased from 0.10 (95% CI 0.07-0.15, 0 m/s) to 0.35 (95% CI 0.29-0.42, 13 m/s),

while search/foraging increased from 0.12 (95% CI 0.09-0.16, 0 m/s) to 0.58 (95% CI

0.51-0.64, 123 m/s).

Transition state probabilities were only weakly influenced by wind speed (see

Supporting information) and ambient light conditions (see Supporting information),

while a small effect was found for rainfall (see Supporting information): the probability

of remaining in a travelling state decreased with increasing rainfall, from 0.86 (95% CI

0.85-0.86, 0 mm/h) to 0.51 (95% CI 0.27-0.75, 6 mm/h) during daytime, and from 0.92

(95% CI 0.91-0.93, 0 mm/h) to 0.61 (95% CI 0.30-0.85, 6 mm/h) during night-time. In

contrast, the probability of transitioning from travelling to search/foraging slightly

increased with increasing rainfall, from 0.14 (95% CI 0.14-0.15, 0 mm/h) to 0.40 (95%

CI 0.17-0.68, 6 mm/h) during daytime, and from 0.07 (95% CI 0.07-0.08, 0 mm/h) to

0.23 (95% CI 0.08-0.50, 6 mm/h) during night-time. The probability to transitioning

from travelling to perching slightly increased with increasing rainfall, but the

confidence interval around mean values was large (see Supporting information).

DISCUSSION

We provide novel evidence for the influence of rainfall on the fine-scale foraging

behavior of a seabird, which we expected to be especially sensitive to rainfall. Foraging

frigatebirds did not avoid areas with rain, nor was there an effect on foraging trip

characteristics. However, when encountering rainfall, individuals modified their activity

patterns, increasing time spent perching and decreasing time devoted to foraging. In

addition, with increasing rain intensity, birds were more likely to switch from travelling

to either perching or foraging/searching. The responses of birds to rainfall were similar

during both daytime and night-time. In contrast, wind speed did not affect behaviors

during daytime. However, during night-time birds engaged more frequently in travelling

and foraging/searching, and spent less time perching with strong winds.

The observed fine-scale response to rainfall suggests that foraging frigatebirds do

not avoid rain by riding storms and flying high above perturbation fronts. In contrast,

birds searched for a perching site above a certain rainfall threshold (~2 mm/h),

presumably to wait until the rain event was over, adopting a strategy that minimizes

energy expenditure and rain exposure. This suggests that the time-activity budget of

frigatebirds during foraging trips is flexible, possibly allowing individuals to buffer the

costs of short-term adverse environmental conditions. This is further supported by the

lack of an overall effect of rainfall on trip characteristics. However, it remains to be

elucidated to what extent such rainfall-mediated reduction of foraging activity affected

chick provisioning rates, and hence chick growth and survival.

Individuals that encountered heavy rainfall while travelling were more likely to

switch not only to perching but also to foraging/searching (despite large CI). This could

be explained by the direct effect of rain on flight mode rather than an actual switch to

foraging: with rainfall, rain drops may force downward momentum of the body,

increasing the power required to stay airborne (Ortega-Jimenez and Dudley, 2012a). In

addition to reduced visibility, this downward force may cause individuals to fly slower

at lower altitudes with higher turning angles, which may appear similar to searching and

foraging behavior. Alternatively, rainfall may cause birds to circle more, as they exploit

maritime cumulous clouds that are associated with thermals and often form in rain

(Rauber et al. 2007). The effect on rainfall on marine fish is still poorly known, but it

has been shown that rainfall events can alter diel rhythm and vertical movements of

fish, resulting in a rain-mediated increased catchability of some species (Payne et al.

2013; Payne et al. 2015). Therefore, we cannot rule out the possibility that the increased

surface-availability of some prey species with rain, coupled with reduced in-air

visibility and increased water turbidity (Corbari et al. 2016), may inhibit the ability of

frigatebirds to spot prey aggregations from high altitudes, causing them to switch to a

lower altitude search mode and increase foraging effort (Ortega et al. 2020). The same

mechanisms appeared to operate during both daytime and night-time. This is consistent

with evidence for night-time foraging in frigatebirds, which are known to scavenge on

fishery discards and target vertically migrating species with the aid of moonlight

(Gilmour et al. 2012) or bioluminescence, and are often on the wing during darkness

(Weimerskirch et al. 2004).

The spatial distribution of foraging frigatebirds was unaffected by rainfall,

implying that birds did not actively avoid perturbation fronts. In an oligotrophic

environment with scattered resources, such as the Caribbean Sea (Longhurst and Pauly

1987; Bertrand et al. 2002), the ability to cover large areas in search of food likely

overrides the need to regularly adapt movements in response to a highly dynamic (and

frequently occurring) environmental component (i.e. rain). Furthermore, the high

probability of perching in heavy rainfall predicted by our model (daytime: 0.98, 95% CI

0.85-1.00; night-time: 1.00, 95% CI 0.99-1.00) may suggest that, when there is a strong

perturbation front, frigatebirds are mostly close to areas where they can rapidly perch.

378 Therefore, despite not avoiding rainfall, their ability to track environmental conditions

379 (Tew-Kai et al. 2009; De Monte et al. 2012; Weimerskirch et al. 2016) could help them

380 sense the arrival of strong perturbation fronts, and pre-emptively position themselves

381 closer to land. Frigatebird associations with mesoscale transport fronts and cumulous

382 clouds (Tew-Kai et al. 2009; De Monte et al. 2012; Weimerskirch et al. 2016) makes

383 them particularly likely to encounter rainfall. Warm ocean eddies can provide heat (and

384 therefore energy) to storms, intensifying them (Wu et al. 2007), and shallow maritime

385 cumulous clouds often form rain (Rauber et al. 2007). Therefore, a mechanism of

386 sensing potentially dangerous perturbation fronts and then moving close to land seems

387 plausible in these species. However, we did not detect an effect of rainfall on distance to

388 the coast at the trip scale (Supporting information). Therefore, if such a mechanism is

389 present, it is likely to operate at a very fine spatial scale that is difficult to detect with

390 our tracking data.

391 The behavioral responses to rainfall were not explained by an increase in wind

392 speed, often linked to barometric depressions that favour rainfall. Rather, wind speed,

393 which was not associated with rainfall in the present dataset, had a distinct effect on

394 behavior during night-time, when individuals were more likely to spend time

395 searching/foraging with increasing wind speed. Since wind facilitates take-off

396 capabilities in seabirds, reducing energy expenditure (Diamond and Schreiber 2002,

397 Shaffer 2011, Clay et al. 2020), frigatebirds could take advantage of it during night-time

398 to become airborne, starting their foraging trips in darkness and commuting to areas

399 where they then forage in higher light conditions.

400 Fully understanding how animals react to environmental conditions, such as rainfall,

401 is important for assessing their resilience to climate change, and it is currently

17

402 considered a research priority in behavioral studies (Buchholz et al. 2019). Severe

403 increases in the rate and extent of rainfall, as well as changes in rainfall seasonality

404 (Feng et al. 2013), are expected to occur in the near future within tropical regions

405 (Collins et al. 2013; Fischer and Knutti 2016). Under this scenario, increasing rainfall

406 rates may disrupt foraging and negatively affect chick survival and fitness. These

407 potential negative effects of rainfall, coupled with predicted increases in extreme

408 climatic events such as hurricanes (Stocker et al. 2013), increasing rates of chick

409 mortality following storms (Schreiber and Burger, 2001) and a wide range of other

410 human-induced pressures, may contribute to threaten frigatebird populations, some of

411 which are already experiencing declines (Birdlife International 2018).

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DATA AVAILABILITY STATEMENT

418 Analyses reported in this article can be reproduced using the data provided by De

419 Pascalis et al. (2021). The data are subject to a delayed-release embargo (12 months),

420 given their use in a large multi-colony collaborative study. During the embargo period,

421 the data are available on Movebank platform (www.movebank.org; Movebank IDs:

422 247401767 & 746405282) upon reasonable request from the corresponding authors.

423 After the embargo period, the data will be freely accessible from Dryad repository.

424

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TABLES

Table 1. Estimated parameters from the fitted three-state Hidden Markov Model. Parameter estimates (means) of step length (kilometers), turning angle (radians) and altitude (meters above sea level) from the fitted three-state HMM, with standard deviation (concentration for turning angle) in parenthesis.

Variable	Searching/foraging	Travelling	Perching
Step length (km)	1.56 (1.30)	4.60 (2.16)	0.01 (0.01)
Turning angle (rad)	-0.02 (1.42)	-0.01 (12.83)	0.03 (0.57)
Altitude (m a.s.l.)	125.63 (112.90)	255.66 (244.88)	23.61 (24.98)

Table 2. AIC comparison of a set of candidate three-state Hidden Markov Models. List of 8 ecologically meaningful candidate models with their AIC and respective difference in AIC (ΔAIC) from the best-fitting model (highlighted in bold).

Model	AIC	ΔAIC
Null model	837378.9	1042.5
Rainfall	837358.7	1022.3
Rainfall + wind speed	837171.1	834.7
Rainfall + wind speed + daytime/night-time	836357.1	20.7
Rainfall + wind speed + daytime/night-time + (rainfall × wind speed)	836367.1	30.7
Rainfall + wind speed + daytime/night-time + (rainfall × daytime/night-time)	836353.2	16.8
Rainfall + wind speed+daytime/night-time + (wind speed × daytime/night-time)	**836336.4**	**0**

FIGURES LEGENDS

704 **Figure 1.** Foraging trips of chick-rearing magnificent frigatebirds. Foraging trips ($n = 517$) of

705 chick-rearing magnificent frigatebirds ($n = 33$) tracked with GPS-GSM loggers during 2017 and

706 2019 from a colony on Little Cayman, Cayman Islands (colony location indicated with a star). Trips

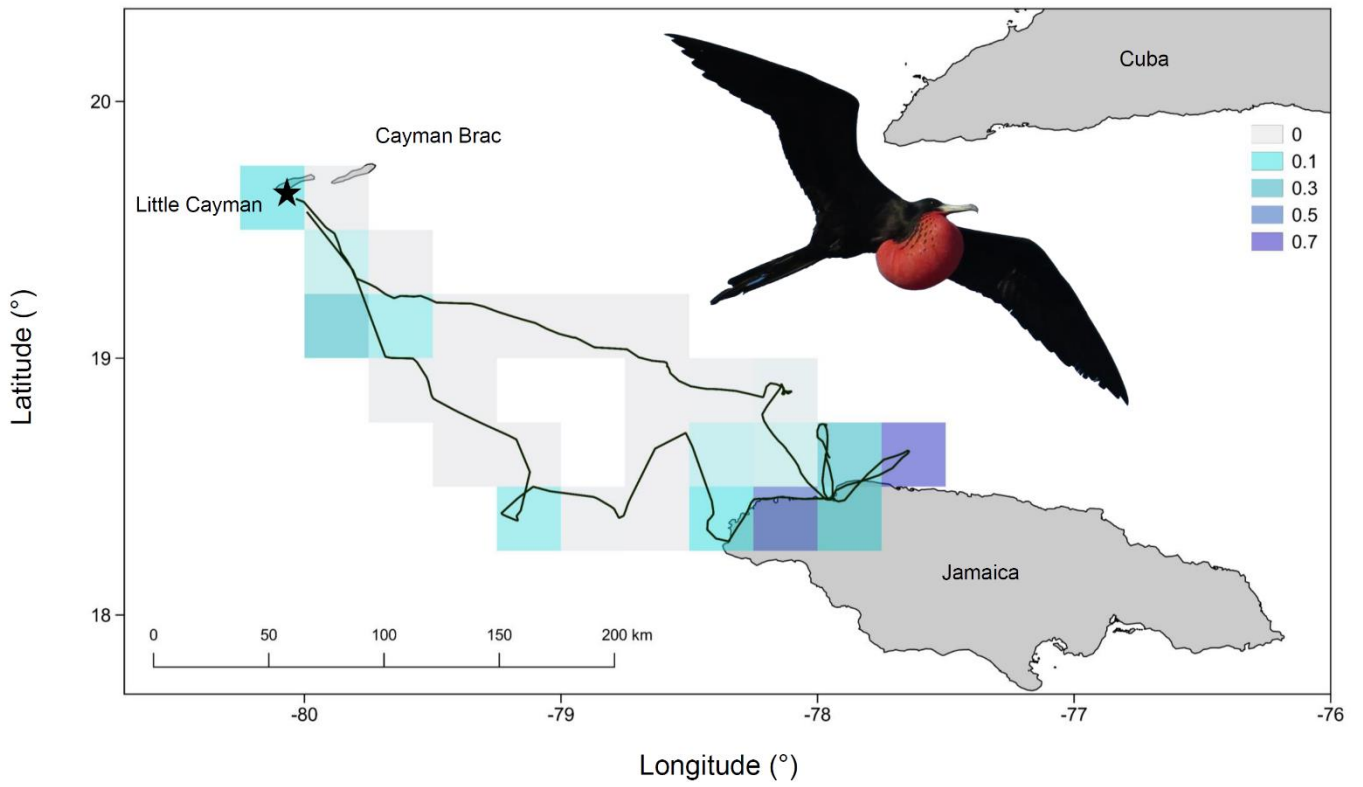707 from different individuals are displayed with different colours.
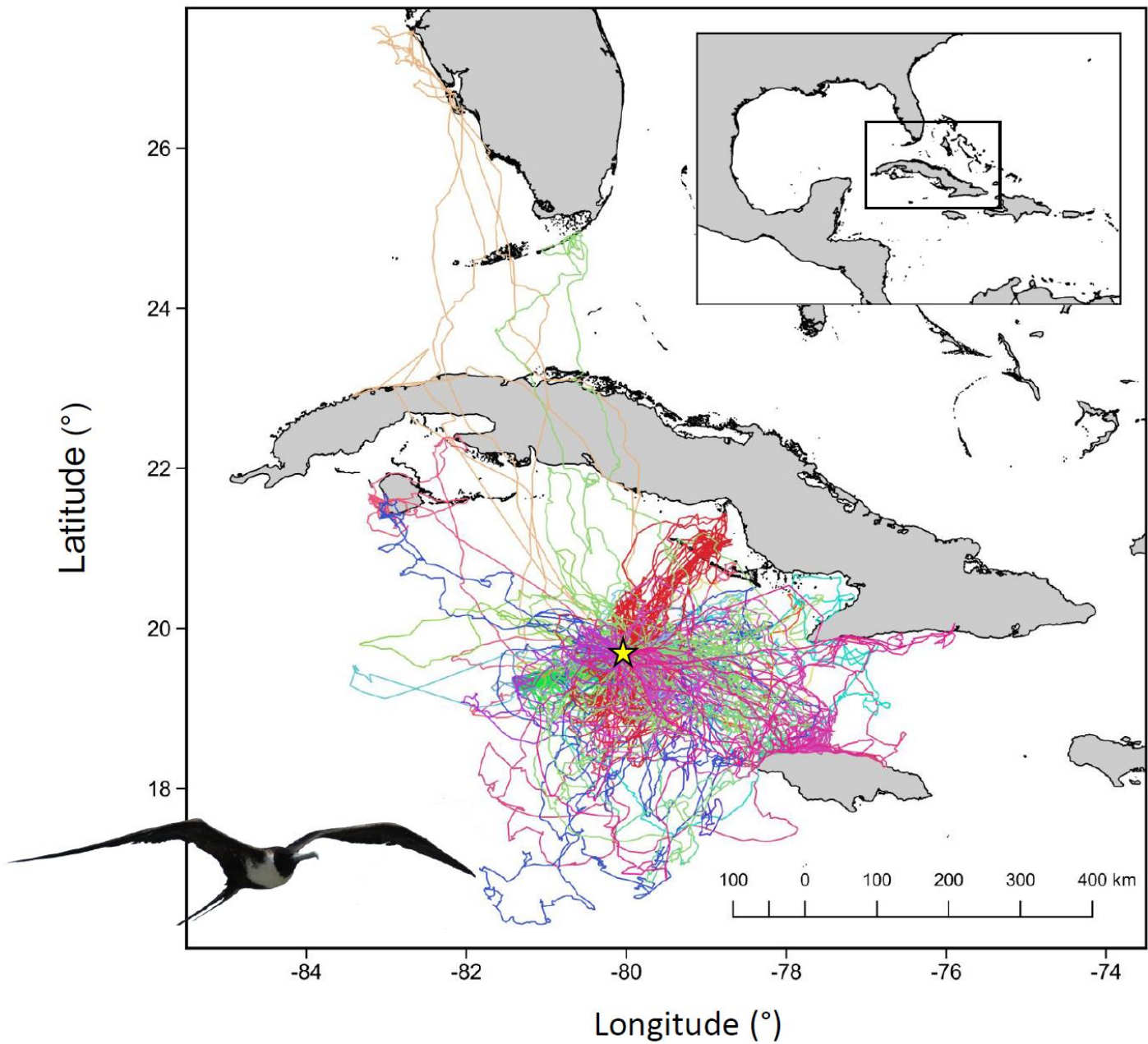
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710 **Figure 2.** Rainfall experienced during a foraging trip of a chick-rearing magnificent frigatebird.

711 Mean rainfall experienced per cell (0.25° x 0.25°) while the bird was present is reported in mm/h.

712 Colony location is represented with a star.
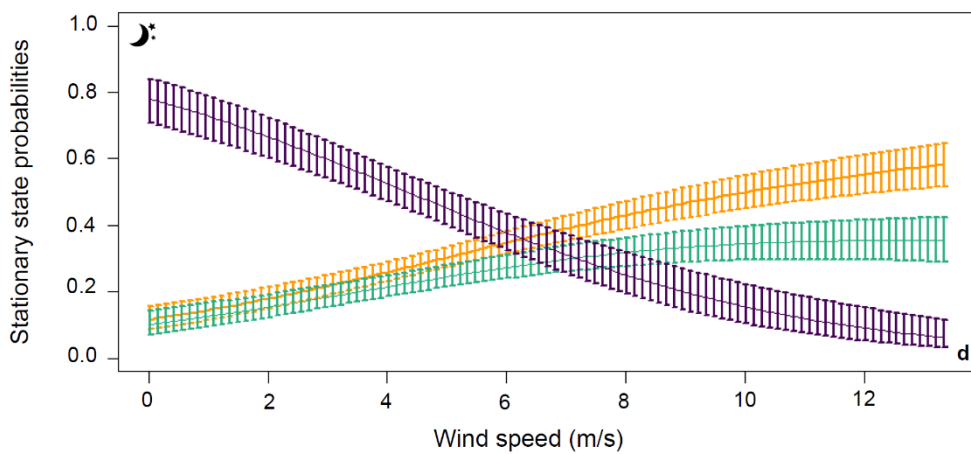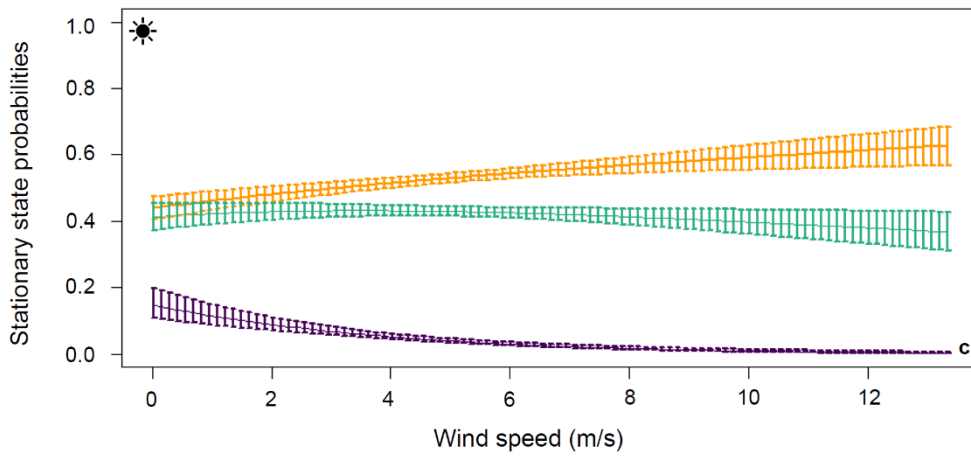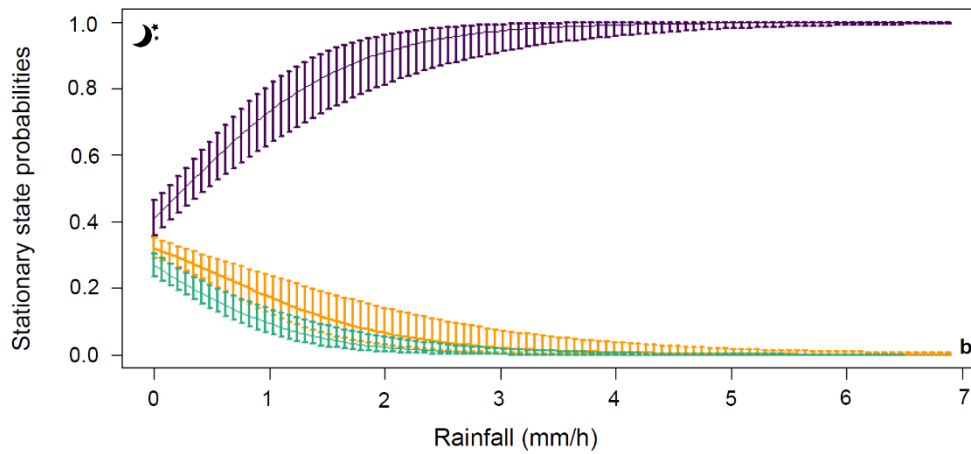

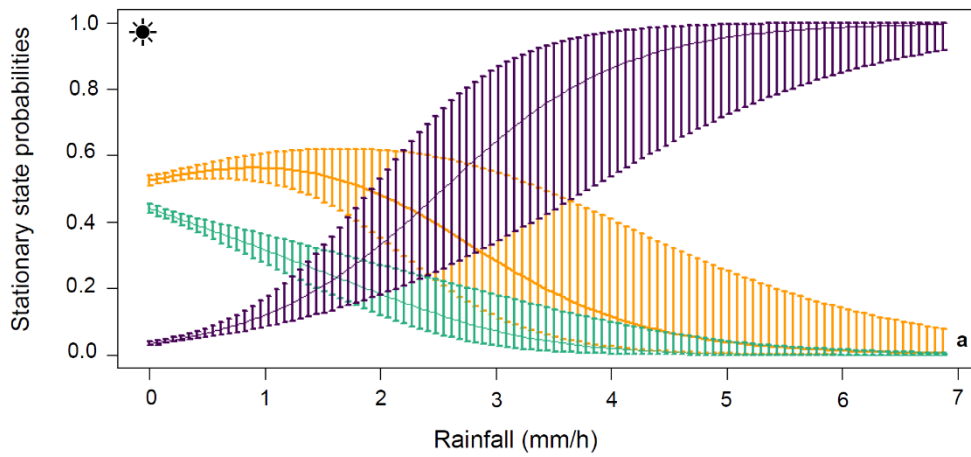
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722   **Figure 3.** Stationary state probabilities for three HMM-estimated behaviors (orange: search/forage,

723   green: travel, purple: perch) with respect to differing rates of rainfall and wind speed (a: daytime

724   rainfall rate, b: night-time rainfall rate, c: daytime wind speed, d: night-time wind speed). Solid

725   lines show means and error bars show 95% confidence intervals. For rainfall plots (panels a & b),

726   wind speed was kept at its mean value (5.11 m/s), and for wind speed plots (panels c - d) rainfall

727   was kept at its mean value (0.09 mm/h).