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1 **The dance of the Cape gannet may contain social information on foraging behaviour**

2

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21 **Abstract**

22 Social information percolates through a variety of channels to influence animal decision-
23 making, with a notable incidence on reproductive and feeding success. Colonial central place
24 foragers can reduce time to locate ephemeral food patches and/or increase foraging rate by
25 following their informed peers, parasitizing direction of returning successful foragers, or
26 being intentionally informed on distant food locations at the colony (e.g., the waggle dance of
27 the honeybee). Ceremonial behaviours may also deliver social foraging information between
28 mates, which can spread inadvertently to neighbours. Here we tested for information display
29 in Cape gannets (*Morus capensis*), a socially monogamous species, during the elaborate dance
30 ceremony performed each time a partner returns to the nest during the breeding season. We
31 tracked fine-scale foraging behaviour of gannets using bird-borne GPS recorders, and video-
32 recorded their subsequent dance ceremony, which involved up to 14 different displays. As we
33 hypothesized, dance characteristics were associated with foraging trip features. Notably,
34 overall dance duration was negatively linked to foraging trip duration, which was highly
35 positively correlated with foraging range, foraging path length and time spent foraging during
36 the trip. Overall dance duration was also negatively linked with distance to the main foraging
37 grounds. Additionally, the duration of the preening behaviour was related to the bearing of the
38 main feeding spot. The latter relationship was supported by a Bayesian model averaging
39 analysis, allowing inferences robust to multiple comparisons. Overall, ceremonial behaviour
40 may provide social foraging information on feeding locations, while evidence for further
41 information transfer to the mate or neighbours was not tested here. Frequent updating on prey
42 spatial distribution, inadvertently communicated or not, should be particularly valuable for
43 predators tracking ephemeral prey patches, providing an additional advantage to colonial
44 living. Our results may have strong implications for cultural evolution in animal societies.

45

46 **Keywords:** Bayesian model averaging, ceremonial dance, foraging movements, GPS
47 tracking, social information, *Morus capensis*, South Africa.

48 Animals may use the behaviour of their surrounding conspecifics or heterospecifics to acquire
49 and update information about the value of alternative options, and are thereby provided with
50 intentionally communicated or inadvertent social information (Danchin, Giraldeau, Valone, &
51 Wagner, 2004; Rieucou & Giraldeau, 2011). Inadvertent social information has initially been
52 observed in foraging situations (e.g. Ward & Zahavi, 1973; Greene, 1987; Valone, 1989),
53 later applied in the context of breeding habitat selection (Boulinier & Danchin, 1997; Doligez,
54 Danchin, & Clobert, 2002), and finally expanded to information about the quality of any
55 feature (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). The use of social
56 information is widespread across animals, including humans, and is predicted to be an
57 essential promoter of cultural evolution (Danchin et al., 2004; Rieucou & Giraldeau, 2011).

58 Social information use is particularly marked in colonial species, where it serves
59 predator defence, defence against brood parasites, behavioural coordination in breeding and
60 migration, breeding habitat selection, sexual and commodity selection, and optimal foraging
61 (Evans, Votier, & Dall, 2016). In the latter case a series of working hypotheses foresee
62 evolutionary benefits to colonial breeding and communal roosting (reviewed in Evans et al.,
63 2016). Notably, these hypotheses propose that individuals provide and share information on
64 the location of food sources (Information Centre Hypothesis: Ward & Zahavi, 1973; Greene,
65 1987). The working hypotheses also posit that individuals benefit from feeding in groups, and
66 hence use colonies to recruit conspecifics (Recruitment Centre Hypothesis: Richner & Heeb,
67 1996; Danchin & Richner, 2001), or suggest that subordinate individuals benefit from
68 information on feeding locations, whereas successful foragers reduce predation risk by
69 occupying safer central positions within the colony (Two-strategies Hypothesis: Weatherhead,
70 1983). Although there is still considerable debate regarding these hypotheses (see the fervent
71 exchanges between Danchin & Richner, 2001; Marzluff & Heinrich, 2001; Richner &
72 Danchin, 2001), uninformed individuals may thereby increase their foraging success, by

73 physically following informed conspecifics towards prey patches (e.g., evening bat *Nycticeius*
74 *humeralis*; Wilkinson, 1992; Eurasian griffon vulture *Gyps fulvus*; Harel, Spiegel, Getz, &
75 Nathan, 2017). Information may also be delivered through visual cues, at the colony or its
76 close proximity, based on flight directions of returning conspecifics (Weimerskirch, Bertrand,
77 Silva, Marques, & Goya, 2010; Racine, Giraldeau, Patenaude-Monette, & Giroux, 2012), or
78 afar the colony when individuals attract each other in the vicinity of food patches (Local
79 Enhancement: Krebs, 1974; Buckley, 1996). This later mechanism has been identified
80 repeatedly in colonial seabirds (e.g., Weimerskirch et al., 2010; Machovsky-Capuska, Hauber,
81 Libby, Amiot, & Raubenheimer, 2014; Thiebault, Mullers, Pistorius, & Tremblay, 2014a;
82 Boyd et al., 2016).

83 Individuals can also benefit from social information without physically following their
84 conspecifics. Notably, some species have evolved signalling for social information transfer.
85 This is famously the case in honeybees (*Apis mellifera*) that inform each other on the location
86 of feeding spots in a complex waggle dance at the hive (von Frisch, 1967; Riley, Greggers,
87 Smith, Reynolds, & Menzel, 2005; Grüter, Balbuena, & Farina, 2008) or in ants (*Lasius*
88 *niger*) and naked mole-rats (*Heterocephalus glaber*) that use scent trails to find food (Judd &
89 Sherman, 1996; Evinson, Petchey, Beckerman, & Ratnieks, 2008). However, it has been far
90 more challenging to establish whether colonial vertebrate animals also provide information
91 about distant foraging grounds through their behaviour at the breeding site in absence of
92 signalling, as recently proposed for seabirds (Weimerskirch, 2013).

93 Some seabirds, such as albatrosses and gannets, are well-known for their elaborate
94 courtship behaviour (Townsend, 1920; Pickering & Berrow, 2001), not only while mating, but
95 also each time one of the partners returns to the nest after a foraging trip at sea (Fig. 1, see
96 Movie A1). The gannet dance ceremony involves a series of displays, eloquently described by
97 Townsend (1920) and later Nelson (1978a). Gannets can vocally identify each other (White,

98 White, & Thorpe, 1970; Krull et al., 2012) and recent studies indicate that they are visually
99 sensitive to coloured signalling of conspecific plumage features, suggesting the importance of
100 observing partners and breeding neighbours in e.g. sexual selection (Ismar et al., 2014). Their
101 high visual capabilities may allow them to recognize each other and to potentially detect the
102 information provided. However, until very recently, gannet dance had only been studied in the
103 context of ecological and evolutionary processes occurring within the breeding colony, such
104 as competition for breeding space and sexual selection (Nelson, 1978b), and sexual and
105 individual recognition (White et al., 1970; Krull et al., 2012). This was probably due to the
106 lack of precise information about the foraging movements of individuals at sea. Thanks to
107 improvement of fine scale-tracking technologies, this gap has now been filled. Notably,
108 Machovsky-Capuska et al. (2014) used Global Positioning System (GPS)-tracking of
109 breeding Australasian gannets (*Morus serrator*) during their trips at sea, to test firstly for
110 linkages between foraging trip characteristics and those of the ceremonial dance displayed
111 upon the birds' return to the nest site. They then tested whether partners leaving the nest used
112 information transferred during the dance. The authors did not find significant relationships,
113 but their study suffered from a small sample size (n = 6 breeding pairs), leaving room for
114 potential type II errors (i.e., falsely infer the absence of true relationships), and from the fact
115 that they reduced the elaborate gannet dance (see Movie A1) to only one display, i.e., the
116 number of bill touches, in addition to dance duration.

117 We therefore repeated these observations with a larger sample size of Cape gannets
118 (*Morus capensis*), also by using high-resolution GPS tracking of bird foraging movements in
119 combination with video recordings of the ceremonial dance displayed upon arrival of GPS-
120 tracked birds at the nest. Here, we focused on the first part of the process of social
121 information transfer (information display). Thereby, considering the whole ceremonial dance
122 complexity, we hypothesized that gannet dance may contain social information related to

123 feeding grounds. Such information should decrease uncertainties in food localization from an
124 evolutionary perspective. We thus expected significant links between foraging trip
125 characteristics and features of the gannet dance ceremony.

126

127 **METHODS**

128 The study was conducted in October-November 2013-2016 on Malgas Island (33.05° S,
129 17.93° E) in the Western Cape, South Africa, which hosts ca. 19 000 breeding pairs of Cape
130 gannets (Crawford, Makhado, Waller, & Whittington, 2014).

131

132 *Ethical Note*

133 All experiments were performed under permit from South African National Parks with respect
134 to animal ethics (N° RYAP/AGR/001—2002/V1).

135 Breeding individuals raising chicks 2-6 weeks' old were caught at the nest and
136 equipped with GPS trackers (CatTrack1, Catnip Technologies, Hong-Kong, PRC, 70×32×15
137 mm, 30 g, 1.2% of a mean bird body mass of 2.5 kg) attached to the lower back with
138 waterproof Tesa® tape only. Indeed, unlike glue which does have an impact on the plumage,
139 tape can be completely removed when recovering the GPS from the bird. Cape gannets are
140 relatively tame at the nest and can be easily caught using a neck-hook mounted on a 3m pole.
141 Once the bird is caught with the pole, it is gently walked away from its nest, to the edge of the
142 colony, where it is caught by hand. The procedure is used twice for each bird (deployment
143 and recovery of the GPS data loggers). Handled birds return straight to their nest when
144 released. Capture may cause momentarily disturbance of the neighbours, which may walk a
145 few steps away from their nests, but also come back onto them within seconds/minutes. We
146 recaptured all birds after 1-3 days, and removed the loggers as well as all tape. We minimized
147 handling stress as much as possible, by handling birds in <10 min, by keeping them whenever

148 possible in the shade to avoid over-heating, and by covering their heads. The fieldwork
149 procedure closely followed Grémillet et al. (2004), who measured no effect of devices on
150 foraging trip duration.

151 GPS-tagged birds were filmed upon their return to the nest. Unlike most northern
152 gannets (*Morus bassanus*), Cape gannets can be approached to a few meters without resulting
153 in any observable effect. Filming and observations, which were performed in the open and
154 away from the edge of the colony, at an approximate distance of 10m, therefore did not
155 disturb any bird of the colony.

156

157 *Foraging Trip Characteristics*

158 We followed the foraging movements of 79 Cape gannets (one individual per breeding pair)
159 using GPS loggers between 2013 and 2016. GPSs recorded position and speed at 30-s to one
160 minute intervals. All GPS tracks were rediscrretized to regular one minute intervals with the
161 *adehabitatLT* package (Calenge, 2006) for the R software (R Core Team, 2016). We only
162 retained foraging trips for which we also had complete video recordings of gannet dance upon
163 their subsequent return to the nest (see *Gannet dance ceremony* section), resulting in a subset
164 of one foraging trip per individual for 28 birds, with 6 birds in 2013, 2 in 2014, 9 in 2015 and
165 11 in 2016 (Fig. 2). Yet, information gathered through GPS tracking, for birds which could
166 not be videoed upon their return, was not lost in any manner since it was used in a long-term
167 monitoring program of Cape gannets as sentinels of environmental change in the Benguela
168 upwelling (e.g. Cohen et al., 2014).

169 We defined a foraging trip as a round trip from the nest of an individual, consisting of
170 all its at-sea GPS locations. We first characterized each foraging trip by its average range (km,
171 i.e., the average distance to the nest across at-sea locations), its maximum range (km, to the
172 farthest at-sea location), its total travelled distance (km, i.e., the cumulative distance between

173 consecutive at-sea locations) and its duration (h). We also calculated time spent in foraging
174 during the trip (min), and the distance (km) and direction (degree) to the main foraging spot,
175 i.e., the average distance and direction from the colony across locations within a single
176 foraging event and constituting the foraging spot where gannet spent most of their time
177 consecutively during the trip. Given the ephemeral nature of food patches at sea, information
178 on the last foraging spot may seem more suitable in a context of information exchange. In our
179 study, the last and main foraging spots were highly correlated both in their direction (circular
180 correlation $r = 0.97$, $N = 28$) and distance (Pearson's correlation $r = 0.64$, $N = 28$) to the
181 colony, and were identical or spatially close (median = 7.5 km, IQR = 0 - 26.3 km, $N = 28$).
182 Therefore, the main foraging spot was a source of both recent and qualitative information
183 (i.e., most valuable patch during the trip inferred from the amount of time spent feeding
184 there). We distinguished the foraging phases from other movement phases (resting and
185 commuting) along the trips with a segmentation-clustering method, which outperforms
186 methods previously and commonly used (Patin, Etienne, Lebarbier, Chamaillé-Jammes, &
187 Benhamou, 2020; see full details in Appendix and Figs A1, A2). To avoid correlation issues,
188 we used only trip duration, distance and direction to the main foraging spot in the subsequent
189 statistical analyses (Appendix Table A1).

190

191 ***Gannet Dance Ceremony***

192 We filmed adult Cape gannets that had been equipped with GPS trackers as they returned to
193 the colony, to document the full dance ceremony upon their arrival at the nest site (see Movie
194 A1). As noted by Machovsky-Capuska et al. (2014) this is extremely challenging, as it
195 requires one to start filming tagged birds *before* they arrive at the nest, their exact time of
196 arrival at the colony being unpredictable. To improve the detection of equipped bird returning
197 to the nest, they were marked with a small blue/red spot (~10cm of diameter) on the head and

198 chest using a biocompatible marker which faded after a few days. Studied birds were selected
199 at random within the colony, and after a sit-and-wait period for the observer, the dance was
200 filmed using a Nikon D90, or a Sony HD Camcorder set on a tripod. We collected a total of
201 79 behavioural sequences for 79 GPS-tagged birds between 2013 and 2016. However,
202 because we missed filming the start of the dance, and/or because the foraging trip was not
203 entirely recorded (rare cases), or both reasons, we retained only 28 complete sequences for
204 which we also had complete GPS-tracking information on the whole preceding at-sea voyage.

205 We considered the dance ceremony in a broad sense (i.e., not only in an inter-sexual
206 context) including all behaviours displayed during changes of guard at the nest between the
207 mates. Our approach allowed us to avoid making a strong a priori hypothesis on the role of
208 the different dance features (i.e., we did not exclude some dancing behaviours potentially
209 implied in an inter-sexual context) and thus avoided potential pitfalls omitting key
210 relationships between dance parameters and foraging features. More specifically, the start of
211 the dance was defined as the time of arrival of the returning gannet at the nest (bird within
212 ≤ 2 m of its partner), either by spot-landing at the nest site, or by landing at a distance and
213 walking towards the nest. The GPS-equipped gannet then displayed some, or all of 14
214 behaviours. “Nape-biting”: one partner grabs the other by the neck and shakes its head
215 sideways. “Scissors/Bowing”: both partners face each other and cross their beaks and heads,
216 moving them repeatedly right and left (i.e., the bill fencing, Fig. 1), regularly interrupting this
217 display to bow towards the ground as in a reverence. “Sky pointing”: the bird stretches its
218 neck, head and beak upwards. “Head-shake”: heads-shake without upward beak, hence
219 different from “Scissors”. “Mutual-preening”: partners preen each other with their beaks.
220 “Preening”: the GPS-equipped bird preens itself. “Shaking”: the GPS-equipped bird ruffles its
221 feathers. “Flapping”: wing-flapping in the GPS-equipped bird. “Chick grooming”: the GPS-
222 equipped bird preens the chick with its beak. “Chick-feeding”: the GPS-equipped bird feeds

223 the chick. “Neighbour fight”: aggressive behaviour of the GPS-equipped bird towards
224 breeding neighbours, in the form of grabbing attempts. “Yawning”: the GPS-equipped bird
225 yawns. “Pause”: none of the other listed behaviours are recorded, and the bird is
226 standing/sitting still. “Changeover”: at some stage during the dance ceremony, the returning
227 (GPS-equipped bird) climbs onto the nest, and takes over chick-guarding duties. The end of
228 the dance ceremony was set when the off-duty partner left the nest (>2m away from the nest),
229 leaving the GPS-equipped bird in charge of chick-guarding. All video analyses were
230 performed by the same person (AVG) with *Avidemux 2.6*, which allows frame-by-frame
231 visualization, and the durations and the start and end times of each behavioural pattern were
232 recorded to the nearest 1/100s. AVG was naïve to the hypothesis tested and blinded to the
233 foraging/travel data.

234

235 ***Linking Foraging Movements and Dancing Behaviour***

236 We tested for the links between foraging movements and dance features based on the 28 birds
237 for which we had both the complete dance ceremony and the entire preceding foraging trip (N
238 = 28). To avoid that correlations among dance ceremony features blurred our understanding
239 of their various relationships with trip features, we proceeded in a two-step approach. First,
240 our aim was to model how dance ceremony duration varied with duration of the previous
241 foraging trip, distance and direction to the main foraging spot. Due to high correlation
242 between foraging covariates (Appendix Table A1), we fitted three independent Cox
243 proportional hazards models (Cox, 1972). Cox regressions were estimated with the *survival*
244 package (*coxph* function; Therneau, 2015) in R software (R Core Team, 2016) and had the
245 form:

$$246 \quad h(\mathbf{t}) = \exp(\beta x) h_0(\mathbf{t}) \quad \text{equation 1}$$

247 where $h(\mathbf{t})$ is the hazard function, i.e., the risk that the dance ceremony ended at time t , \mathbf{t} is a

248 vector, β is the estimated coefficient for the continuous foraging trip covariate x , and $h_0(\mathbf{t})$ is
 249 an unspecified baseline hazard function. The proportional hazard assumption was satisfied for
 250 each regression. We accounted for multiple comparisons using Benjamini-Yekutieli
 251 corrections (Benjamini & Yekutieli, 2001). For more convenience in interpretation, we
 252 present in the results the predicted total duration of the dance ceremony (not the risk of
 253 terminating the dance) given the foraging covariates, i.e., the duration-based quantities
 254 estimated from Cox regression with the *coxed* package (*coxed* function; Kropko & Harden,
 255 2020).

256 Second, we used Bayesian Model Averaging (BMA) analyses to evaluate relationships
 257 between the patterns of the foraging trips and those of the dance ceremony. To avoid
 258 overfitting models, we only considered candidate models with three or fewer predictors. We
 259 took advantage of the BMA framework to robustly average the nonetheless numerous
 260 candidate models and get accurate final models. BMA accounts for the model uncertainty
 261 inherent in the variable selection problem, by averaging posterior distributions under each
 262 candidate model M_k , weighted by posterior model probabilities $\pi(M_k|y_N)$ (Raftery, 1995;
 263 Hoeting, Madigan, Raftery, & Volinsky, 1999; Neath, Flores, & Cavanaugh, 2018). For a
 264 candidate collection with L models and given data y_N , the Bayesian posterior probability on
 265 model M_k is approximated by:

$$266 \quad \pi(M_k|y_N) = \frac{\exp(-\Delta B_k/2)}{\sum_{l=1}^L \exp(-\Delta B_l/2)}, \quad \text{equation 2}$$

267 where B_k is the Bayesian information criterion (BIC; Schwarz, 1978) for the model M_k and
 268 $\Delta B_k = B_k - \min B_l$. Bayesian model parameter estimates and Bayesian interval estimates for
 269 a mean μ_i for predictor i are based on the mixture distribution:

$$270 \quad f(\mu_i|y_N) = \sum_{l=1}^L f(\mu_i|M_k, y_N) \times \pi(M_k|y_N), \quad \text{equation 3}$$

271 where $f(\mu_i|M_k, y_N)$ is the posterior distribution on μ_i given data y_N under model M_k . Since
 272 the relative weight $\pi(M_k|y_N)$ on each model may decrease as the set of candidate models

273 grow larger, the use of BIC weights as posterior probabilities allows valid multiple
274 comparisons in a BMA framework (Neath et al., 2018). The number of candidate models
275 being rapidly high ($2^{\text{number of predictors}}$) in a model averaging process, BMA uses the leaps and
276 bounds algorithm (Furnival & Wilson, 1974) and an Occam's window to retain a set of 'best'
277 candidate models (Volinsky, Madigan, Raftery, & Kronmal, 1997; Hoeting et al., 1999).

278 We conducted three distinct BMA analyses, using either BMA for Cox proportional
279 hazards models for the *Trip duration* response variable, or using BMA for linear models for
280 *Distance to the main foraging spot* and *Direction to the main foraging spot* response
281 variables. *Distance to the main foraging spot* was log transformed to satisfy normality of
282 residuals. Considering the high correlation between some foraging trip features ($r \geq 0.7$, $N =$
283 28; Appendix Table A1), we limited our analyses to the effect of dance ceremony patterns on
284 these three key parameters of foraging trips, commonly used. We considered direction to the
285 main foraging spot as a linear (not circular) dependent variable because colony was settled
286 along an approximate straight coastline (Fig. 2). Consequently, no high direction values
287 occurred (max = 209°) and values had a range close to 180° (range was of 195°). We
288 characterized gannet dance patterns by the proportions of time spent in eight different
289 behaviours (i.e., chick grooming, change over, head shake, scissor bowing, nape bite, mutual
290 preening, individual preening and sky pointing) and used them as predictors (Appendix
291 Tables A2 and A3). We excluded behaviours that represented <1%, on average, of dance
292 duration, and the proportion of time spent to rest (pause behaviour) from BMA analyses
293 (Appendix Tables A3 and A4). All predictors were mean-centred and scaled. Candidate
294 models selected by BMA did not contain strongly correlated predictors ($r < 0.7$, $N = 28$;
295 Appendix Tables A2 and A5). All predictors had an equal weight of 0.5 a priori. Finally, we
296 calculated a sharp confidence interval of 99% for Bayesian parameter estimates, to account
297 for the fact that three BMA analyses were fitted from the same set of predictors. BMA was

298 performed with the *BMA* package (Raftery, Hoeting, Volinsky, Painter, & Yeung, 2018) and
299 *BAS* package (Clyde, Littman, Wang, Ghosh, & Li, 2018) for the R software (R Core Team,
300 2016).

301

302 **RESULTS**

303 *Foraging Trip and Dance Ceremony Characteristics*

304 Average values showed that GPS-tracked Cape gannets foraged within 108 km of the
305 breeding colony, mainly to the West and the South, and travelling on average 346 km during
306 trips lasting 22 h (Fig. 2, full details on foraging parameters are provided in Appendix Table
307 A4). Birds met their main foraging spot on average at 77 km from the colony, and displayed
308 active foraging for 6.45 h across their trip (Fig. 2). Trip duration was highly positively
309 correlated with foraging range, foraging path length and time spent in foraging during the trip
310 (Appendix Table A1). Classification of the different behavioural modes were consistent with
311 biological expectations, and we found that gannet moved with high tortuosity and average
312 mean smoothed speed of 16.81 km.h⁻¹ during the feeding phases (see full details in Appendix
313 and Figs A1, A2).

314 On average, upon their return to the nest, birds displayed a dance ceremony which
315 lasted 5.7 min, with, by order of importance in terms of time, 60.1 s of individual preening
316 (13% of total dance duration on average), 45.2 s of mutual preening (9%), 44.0 s of
317 scissors/bowings (23%), 10.8 s of head shaking (4%), 7.9 s of chick grooming (2%), 6.7 s of
318 sky pointing (2%), 2.3 s of chick feeding (<1%), 1.3 s of nape biting (<1%), 1.0 s of wing
319 flapping (<1%), 0.8 s of shaking (<1%), 0.4 s of neighbour fighting (<1%), 0.3 s of yawning
320 (<1%), and 156 s in pause (43%; Appendix Table A4).

321

322 *Evidence for Related Foraging Movements and Dancing Behaviour*

323 Dance ceremony duration was negatively linked to the duration of the previous foraging trip,
324 with a decrease of ~11 s (range 15 to <1 s) in dance duration for each additional hour spent at
325 sea (Fig. 3a, Appendix Table A6). Dance duration also decreased with an increase of the
326 distance to the main foraging spot, with a decrease of ~2 s (range 3 to 1 s) in dance duration
327 for each supplementary kilometre between the nest and the main feeding area (Fig. 3b,
328 Appendix Table A6).

329 Each BMA analysis indicated moderate model uncertainty (highest posterior model
330 probability was 0.134 for trip duration model, 0.260 for the distance to the main foraging spot
331 model, and 0.331 for the direction to the main foraging spot model, Appendix Table A5),
332 emphasizing the need to consider it within a BMA framework for robust inferences. Trip
333 duration not only impacted dance duration, but also the structural properties of the dance
334 ceremony. Thereby, the average model for trip duration indicated a posterior effect
335 probability of 0.978 for the scissors/bowings predictor (Appendix Table A3). Gannets spent
336 higher proportion of their dance ceremony displaying scissors/bowings movement heads
337 when the foraging trip duration increased (i.e., when the risk of returning to the nest was low;
338 Fig. 4a, Appendix Table A3). Considering that an increase in foraging trip duration was
339 related to a decrease in dance duration and an increase in the proportion of scissors/bowings,
340 gannet seemed to spend an incompressible amount of time displaying scissors/bowings during
341 the dance ceremony. Consistently, dance duration was uncorrelated with the total time spent
342 in scissors/bowings ($r = 0.06$, $N = 28$, $P = 0.75$), a variable with a relatively low dispersion
343 (Appendix Table A4), but was negatively correlated with the proportion of time in
344 scissors/bowings ($r = -0.58$, $N = 28$, $P = 0.001$). Trip duration was not related to any other
345 features of dance ceremony.

346 Distance to the main foraging spot had no significant impact on the proportions of the
347 different behaviours displayed during the dance ceremony (Appendix Table A3). In contrast,

348 individual preening behaviour might be an indicator of the direction to the main foraging spot.
349 Indeed, gannets spent a lower proportion of their time preening during the dance ceremony
350 when they had mainly foraged to the South than to the West of the colony (Fig. 4b, Appendix
351 Table A3). This result was supported by a posterior effect probability of 1.000 for the
352 individual preening predictor (Appendix Table A3). Importantly, the direction to the main
353 foraging spot was not related to dance duration ($r = -0.32$, $N = 28$, $P = 0.09$). Using a
354 principal component analysis confirmed the results of BMAs (Appendix Fig. A3).

355

356 **DISCUSSION**

357 We identified significant linkages between at-sea Cape gannet foraging movements and their
358 subsequent dance ceremony when returning to the nest site, using a two-step analytical
359 framework robust to multiple comparisons. Notably, we found that dance ceremony is an
360 indicator of foraging effort and direction and distance to the recent and most used prey patch
361 visited during the last trip. It is, to the best of our knowledge, the first evidence that
362 ceremonial behaviour might be a channel of social foraging information on distant feeding
363 locations at a vertebrate breeding aggregation. Our correlative approach did not allow testing
364 whether dance features constitute social information per se. Indeed, this information is
365 probably supplied inadvertently through the dance; yet, we do not know if the mate and
366 neighbours receive and use the foraging information displayed during the dance.

367

368 ***Gannet Dance Could Socially Inform Conspecifics on Prey Patch Location***

369 Overall dance duration decreased with increasing duration of the preceding foraging trip and
370 distance to the main foraging spot. Gannet foraging trip duration is tightly linked to structural
371 (foraging range and foraging path length) and functional (time spent in foraging during the
372 trip; Appendix Table A1) trip features, and hence a reliable proxy for foraging effort (Lewis,

373 Sherratt, Hamer, & Wanless, 2001). Shorter dancing duration could constitute a social cue for
374 conspecifics, of how hard gannets foraged at sea and at which distance they mainly fed.

375 The negative correlation between the dance duration and the duration of the preceding
376 foraging trip also suggests that the partner which had been staying at the nest of the GPS-
377 equipped bird to guard their chick was in a hurry to start its own foraging sequence and/or
378 that the incoming bird was exhausted, and each second seemed to count in that respect. This
379 starvation hypothesis of the waiting partner (or exhaustion hypothesis of the incoming bird)
380 may be reinforced by the fact that the variance in dance duration was much greater for short
381 and medium foraging trip durations (Fig. 3a). Overall, even if the hungry state of the waiting
382 partner is the main mechanism driving dance duration, the outcome information of the dance
383 remains the same for the potentially eavesdropping neighbours: short dance duration
384 corresponds to long at-sea foraging trip. Cape gannets competing with fisheries are
385 experiencing nutritional stress leading to lower body condition (Grémillet et al., 2016). If
386 birds are in a hurry to feed this may lead to a reduction in time available for information
387 displays at the colony, which in turn may trigger a negative feedback loop on their
388 population-level foraging performance. This negative feedback could be enhanced by the fact
389 that an incompressible part of the ceremonial dance seems to be dedicated to scissors/bowing
390 behaviour. This incompressibility of scissors/bowing behaviour reveals a key parameter of the
391 gannet dance, perhaps more related to courtship display (Townsend, 1920), pair bonding
392 (Nelson, 1978b), mate recognition (Meseth, 1975) or individual's condition assessment rather
393 than foraging information display, echoing previous work by Machovsky-Capuska et al.
394 (2014).

395 Moreover, gannets preened more during the dance ceremony when they had travelled
396 to the West than to the South. By preening, gannet may convey inadvertent cues on food
397 patches direction to others. Such differences in preening behaviour might be explained by the

398 fact that Cape gannets from the study colony preferentially target sardines and avoid purse-
399 seine fishing vessels when foraging in the South of their at-sea home-range, and feed on
400 fishery wastes behind hake trawlers when foraging to the West (Tew-Kai et al., 2013). Indeed,
401 birds attending trawlers are more likely to get into contact with fish oil and other elements
402 affecting their plumage, and we speculate that this might then lead Cape gannets to preen
403 more often. Nevertheless, for the partner or neighbours observing the displaying individual,
404 deducting the direction to the main foraging spot from preening behaviour requires strong
405 cognitive abilities (e.g., associative learning, memory), which remain to be measured in
406 seabirds.

407 One important condition for the emergence of social information is the temporal match
408 between the duration of a prey patch occurrence in the environment and the time required for
409 an informed conspecific to revisit the patch. If prey patches disappear before conspecifics can
410 revisit the patches, information on patch location is useless. The duration of a prey patch is
411 highly variable in our study area, and the number of prey patches is probably more limiting
412 than the size of individual patches, thereby determining encounter rates of Cape gannets with
413 their prey (Discussed in Thiebault, Semeria, Lett, & Tremblay, 2016). We found that the main
414 foraging patch is also often the last foraging patch, or at least close to it, and hence gannet
415 dance provides recently updated information (median time elapsed since departure from the
416 main foraging spot was 2.4h). When prey patches occur for sufficiently long time, allowing
417 the same individual to revisit them, sharing information is still valuable if predators forage
418 more efficiently in groups (Danchin & Richner, 2001), as it is the case for northern and Cape
419 gannets (Wakefield et al., 2013; Thiebault et al., 2016).

420 Conspecifics may also acquire some information from the dance ceremony by
421 observing for how long their neighbours are away at sea, yet this requires keeping track of
422 time at the scale of hours, even days, something which will not always be possible since those

423 neighbours may also have to leave the colony to forage in the meantime. Contrastingly, the
424 dance ceremony provides inadvertent information on a wide range of foraging parameters
425 within just a few minutes. Considering the large number of available neighbours at our Cape
426 gannet study colony, the accumulation of easily-observable dance ceremonies could then
427 provide permanently-updated robust knowledge on foraging grounds within the colony-
428 specific home-range, depending on oceanographic conditions.

429

430 *On the Relevance of Information Displays*

431 Yet, signals on foraging behaviour provided during the dance of the Cape gannet are far less
432 subtle and detailed than those generated by honeybees and other insects, which may actively
433 provide the accurate direction and distance to the resource, but also information on its
434 chemical properties (Riley et al., 2005; Leadbeater & Chittka, 2007; Grüter et al., 2008).
435 Further, despite all our efforts to gain an adequate sample size, the statistical power of some
436 of our analyses may remain limited. Distinguishing between inadvertent (as suggested here)
437 and intentional information display through the gannet dance is therefore particularly
438 challenging. Moreover, foraging information contained in gannet dance might be only
439 relevant if it is actually used by birds (mate or neighbours), and a previous study on ring-
440 billed gull (*Larus delawarensis*) showed that information provided by leaving and arrival
441 flight direction of conspecifics was irrelevant at the colony (Racine et al., 2012). These
442 aspects should be tested through further studies, in vertebrate species performing behavioural
443 ceremonies following, or preceding, foraging activity. To go beyond our correlative approach
444 these studies should, ideally, be experimental (Reader & Biro, 2010), testing for example if
445 dancing behaviour facilitates localization of foraging grounds, by following each individual in
446 the pairs with GPS (Machovsky-Capuska et al., 2014), or testing if the starvation state of the
447 waiting partner mainly drives dance duration, with a food supplementation experiment. Also,

448 the dance ceremony could provide feedback on the nutritional state (e.g., body condition,
449 coloration) of the foraging partner (Machovsky-Capuska et al., 2016) or be tightly linked to
450 the sex-specific foraging behaviour of gannets (not in trip duration but possibly in feeding
451 areas; Lewis et al., 2002).

452

453 ***Social Foraging Information Percolates from Multiple Pathways in Seabirds***

454 Our results echo recent work demonstrating that Cape gannets use social information *en route*
455 to their feeding sites and gannets anticipate the spatio-temporal occurrence of their prey
456 (Pettex, Bonadonna, Enstipp, Siorat, & Grémillet, 2010). For instance, investigations
457 combining GPS-tracking with bird-borne video recordings demonstrated that gannets which
458 reacted to the presence of conspecifics during their initial flight from the colony to a food
459 patch reached this patch twice as fast as those which did not make use of social information
460 (Thiebault et al., 2014b). This following behaviour has also been clearly established in
461 vultures (Harel et al., 2017) and is known to reduce searching time in uninformed ant
462 individuals (Franks & Richardson, 2006).

463 Further, our findings are highly coherent with a growing body of work explaining
464 foraging spatial asymmetries in seabirds through the use of social information, available at the
465 breeding colony and/or at sea. Specifically, Grémillet et al. (2004) noticed that GPS-tracked
466 Cape gannets from neighbouring colonies had mutually exclusive at-sea home ranges during
467 the breeding season, even when neutral diffusion models predicted that those areas should
468 overlap widely. The authors termed this system ‘Offshore diplomacy’, and their observations
469 have meanwhile been confirmed in a large number of seabird species. Notably, Wakefield et
470 al. (2013) found mutually-exclusive at-sea home ranges across 12 breeding colonies of
471 northern gannets around the British Isles, pointing to space partitioning without territoriality.
472 The authors developed individual-based models of gannet foraging distributions, which

473 strongly suggested the importance of bird memory and social information for the emergence
474 of foraging asymmetries leading to offshore diplomacy. They speculated that information
475 must be made public, probably inadvertently, by birds at sea and at the breeding site, but did
476 not propose specific behavioural pathways. Our findings indicate that the dance of the gannet
477 may convey social information to the partners and neighbours of gannets returning from the
478 sea. This information channel seems particularly likely and pertinent, since Cape gannets have
479 one of the highest breeding densities of any seabird, with on average 3 nests per square meter
480 (Randall & Ross, 1979). The use of multiple social information pathways could offer a
481 selective advantage to colonial species, as it could minimize uncertainty in locating ephemeral
482 prey patches (Harel et al., 2017; Courbin et al., 2018). Overall, insights gained through our
483 study open exciting perspectives with respect to the emergence of coloniality (Danchin et al.,
484 2004; Rieucou & Giraldeau, 2011; Evans et al., 2016).

485

486 **Author Contributions**

487 DG designed the study; NC designed and conducted the statistical analyses; DG, CP, TC, and
488 LP collected field data; PGR supervised TC; AVG analyzed the videos; NC and DG drafted
489 the manuscript; All authors contributed to the writing. All authors gave final approval for
490 publication.

491

492 **Competing Interests**

493 No competing interests declared.

494

495 **Data Availability**

496 Data are available online at <https://mycore.core-cloud.net/index.php/s/44d1PNWFE1d7wiW>.

497

498 **Supplementary Material**

499 Movie A1 is available online at [https://mycore.core-](https://mycore.core-cloud.net/index.php/s/IuxM0jHCjdHVNuo)
500 [cloud.net/index.php/s/IuxM0jHCjdHVNuo](https://mycore.core-cloud.net/index.php/s/IuxM0jHCjdHVNuo)

501

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511

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680

681 **Appendix**

682 **Identification of behavioural modes with segmentation-clustering method**

683 We assumed that a foraging trip is composed by the succession of homogeneous bouts in
684 terms of speed and sinuosity (stationary phases along the signal). We looked for phases that
685 are stationary in terms of these metrics (i.e. characterized by a roughly constant mean and
686 variance, different from those of the previous and next phases; Benhamou, 2014). In the
687 present study, we considered that these phases corresponded to three types of behavioural
688 mode: transiting, feeding and resting. They were identified using a segmentation-clustering
689 method (Patin et al., 2020) applied to two metrics simultaneously: the smoothed speed (i.e.,
690 speed smoothed over two steps before and after the focus location) and the turning angle
691 measured at constant step length (i.e., angle between the focus location, the first location
692 entering a circle of radius equal to the median step length, and the last location inside the
693 circle), which were showed to provide the best contrast between the behavioural modes
694 considered. This method both segments the bivariate signal provided by the two metrics into
695 stationary phases and assigns the phases to one out of the three behavioural modes
696 considered, as a Hidden Markov model-based approach would do, but in way that is both
697 simpler and less sensitive to random noise (Patin et al., 2020). Considering that gannets rest at
698 sea surface and that current velocities change in space and time, the segmentation-clustering
699 ability of the method decreased with the length of the time-series (i.e., the duration of the
700 foraging trip). Indeed, we observed a higher likelihood to classify separately resting phases
701 with different speed and merge the transiting and feeding phases (i.e., identification of two
702 resting phases and one global movement mode). To compensate this artefact, we therefore
703 allowed four modes in the segmentation-clustering analysis, and grouped them later into the
704 three expected behaviours (Appendix Fig. A1). Behavioural mode identification was

705 performed with the *segclust2d* package (Patin, Etienne, Lebarbier, & Benhamou, 2018) for R
706 software (R Core Team, 2016), with *Lmin* set to 5 locations.

707 Consistently with biological expectations, we found that Cape gannet moved with high
708 tortuosity and moderate speed during the feeding phases (average SD of turning angle of
709 feeding clusters was of 1.28 rad and average mean smoothed speed of feeding clusters was of
710 16.81 km.h⁻¹), with lower tortuosity and lower speed during the resting movement bouts
711 (average SD of turning angle was of 0.27 rad and average mean speed was of 1.63 km.h⁻¹),
712 and transited using movements with lower tortuosity and higher speed (average SD of turning
713 angle was of 0.23 rad and average mean speed was of 47.32 km.h⁻¹; Appendix Fig. A2).

714 Table A1. Pearson's correlation coefficients among the features of the foraging trips of Cape gannets.

	Avg.range	Max.range	Tot.distance	Duration	Dist.spot	Dir.spot	Time.in.foraging
Avg.range	1	0.95***	0.86***	0.79***	0.85***	0.57**	0.58**
Max.range		1	0.82***	0.72***	0.81***	0.57**	0.47*
Tot.distance			1	0.96***	0.64***	0.44*	0.81***
Duration				1	0.60***	0.39*	0.86***
Dist.spot					1	0.71***	0.38*
Dir.spot						1	0.29

715 NB: avg.range = the average range of the trip in km, max.range = the maximum distance reached during the trip in km, tot.distance = the total
716 travelled distance moved during the trip in km, duration = the time of the trip in hour, dist.spot = the distance to the main foraging spot in km,
717 dir.spot = the direction to the main foraging spot in degree, time_in_foraging = the total time spent in foraging during the trip in hour. *** means
718 $P < 0.001$, ** means $P < 0.01$, * means $P < 0.05$. The variables used in the statistical analyses are shown in bold.

719 Table A2. Pearson's correlation coefficients among the features of the Cape gannet dance.

	Duration	Chick feeding	Chick grooming	Change over	Flapping	Head shaking	Mutual preening	Nape bite	Neighbour fight	Individual preening	Pause	Scissors bowing	Shaking	Sky pointing	Yawning
Duration	1	0.20	-0.01	-0.48**	-0.11	-0.28	0.55**	-0.34	0.60***	0.44*	0.20	-0.58**	-0.04	0.12	0.13
Chick feeding		1	-0.08	-0.09	0.08	-0.28	-0.30	-0.17	0.43*	-0.10	0.36	-0.10	-0.17	0.13	-0.10
Chick grooming			1	-0.18	-0.16	0.44*	0.09	-0.11	-0.09	-0.03	-0.14	-0.07	-0.03	-0.12	0.30
Change over				1	0.51**	0.17	-0.23	0.29	-0.22	-0.29	-0.19	0.26	0.11	-0.03	-0.09
Flapping					1	-0.09	0.07	0.39*	0.06	-0.15	0.07	-0.14	-0.15	0.08	-0.08
Head shaking						1	-0.16	0.02	-0.05	-0.19	-0.17	0.14	0.32	-0.06	0.27
Mutual preening							1	-0.09	-0.01	0.22	-0.08	-0.46*	-0.13	-0.19	0.45*
Nape bite								1	-0.11	-0.24	0.16	-0.07	-0.07	-0.14	-0.07
Neighbour fight									1	0.11	0.13	-0.18	-0.10	0.35	-0.07
Individual preening										1	-0.24	-0.43*	0.32	0.23	<0.01
Pause											1	-0.63***	-0.07	-0.10	-0.15
Scissors/bowing												1	-0.12	-0.05	-0.14
Shaking													1	0.07	0.03
Sky pointing														1	-0.10

720 NB: Duration = the time of the dance in s. The proportions of time spent in one of the 14 recorded activities are also indicated: chick feeding,

721 chick grooming, change over, flapping, head shaking, mutual preening, nape bite, neighbour fight, individual preening, pause, scissors/bowing

722 head movements, shaking, sky pointing and yawning

723 Table A3. Bayesian model averaging (BMA) assessing the relationships between the
724 structural properties of Cape gannet dance ceremony and of the previous foraging trip,
725 between 2013 and 2016, with the posterior mean estimates (Mean ($\beta | y_N$)), standard
726 deviations (SD ($\beta | y_N$)), 99% confidence intervals (99% CI ($\beta | y_N$)) and the posterior effect
727 probability ($P(\beta \neq 0 | y_N)$), for each variable and given data y_N .

	Mean (βy_N)	SD (βy_N)	99% CI (βy_N)	Posterior effect probability, $P(\beta \neq 0 y_N)$
<i>Trip duration model</i>				
Chick grooming	-0.04	0.13	-0.60;0.32	0.149
Change over	-0.02	0.12	-0.70;0.22	0.105
Head shake	0.14	0.25	-0.03;1.01	0.351
Scissor Bowing	-0.93*	0.40	-1.79;-0.14	0.978
Nape bite	0.14	0.23	0.00;0.82	0.349
Mutual preening	0.07	0.18	-0.01;0.71	0.213
Individual preening	-0.01	0.07	-0.28;0.51	0.084
Sky pointing	0.02	0.09	-0.30;0.49	0.127
<i>Log(Distance to the main foraging spot model)</i>				
Intercept	4.17*	0.09	3.94;4.44	1.000
Chick grooming	0.001	0.02	-0.12;0.12	0.039
Change over	<0.001	0.02	-0.07;0.12	0.024
Head shake	-0.19	0.13	-0.48;0.05	0.815
Scissor Bowing	0.05	0.11	-0.02;0.43	0.272
Nape bite	-0.001	0.02	-0.12;0.02	0.027
Mutual preening	-0.11	0.13	-0.45;0.05	0.514
Individual preening	-0.17	0.14	-0.51;0.02	0.689

Sky pointing	-0.008	0.04	-0.26;0.06	0.083
<i>Direction to the main foraging spot model</i>				
Intercept	147.29*	6.82	128.23;166.30	1.000
Chick grooming	0.59	2.97	-4.05;19.53	0.073
Change over	-0.15	1.72	-12.99;5.65	0.047
Head shake	-17.47	8.89	-39.29;0.69	0.907
Scissor Bowing	0.81	3.47	-3.21;21.96	0.087
Nape bite	-0.33	2.17	-16.04;4.18	0.058
Mutual preening	-5.20	8.14	-31.41;2.39	0.363
Individual preening	-32.92*	7.52	-53.46;-11.76	1.000
Sky pointing	0.94	3.57	-3.81;21.08	0.107

728 * 99% CI excluded 0. Note that parameter estimates, SD, and 99% CI directly incorporate
729 model uncertainty.

730 Table A4. Summary statistics for the dance ceremony patterns and the foraging trip patterns.

	Mean	SD	Range
<i>Foraging trip pattern</i>			
Average range (in km)	72.16	35.20	21.78 ; 138.25
Maximum range (in km)	102.88	51.06	29.34 ; 208.83
Total travelled distance (in km)	346.37	213.51	88.08 ; 1083.33
Duration (in h)	22.36	16.23	3.02 ; 78.67
Distance to the main foraging spot (in km)	76.75	46.74	25.62 ; 180.90
Direction to the main foraging spot (in degree)†	152.75*	49.45*	13.42 ; 208.72
Time in foraging (in min)	386.82	280.65	66 ; 1432
<i>Dance ceremony pattern</i>			
Total time of dance ceremony (in s)	341.89	258.17	39.08 ; 996.48
Time in pause (in s)	155.95	153.24	0.00 ; 621.56
Time in preening (in s)	60.07	87.57	0.00 ; 384.28
Time in mutual preening (in s)	45.15	74.69	0.00 ; 272.84
Time in scissor / bowing (in s)	43.96	23.63	3.48 ; 100.00
Time in head shake (in s)	10.82	9.89	0.00 ; 35.92
Time in chick grooming (in s)	7.86	12.15	0.00 ; 46.28
Time in sky pointing (in s)	6.66	14.68	0.00 ; 70.16
Time in changeover (in s)	5.16	5.05	0.00 ; 17.24
Time in chick feeding (in s)	2.26	7.15	0.00 ; 31.64
Time in nape bite (in s)	1.33	1.85	0.00 ; 6.48
Time in flapping (in s)	1.00	2.12	0.00 ; 8.04
Time in shaking (in s)	0.78	1.48	0.00 ; 6.8
Time in neighbour fight (in s)	0.42	1.51	0.00 ; 7.8

Time in yawning (in s)	0.26	1.23	0.00 ; 6.48
Proportion of time in pause	0.43	0.21	0.00 ; 0.84
Proportion of time in scissor / bowing	0.23	0.25	0.02 ; 1.00
Proportion of time in preening	0.13	0.15	0.00 ; 0.51
Proportion of time in mutual preening	0.09	0.12	0.00 ; 0.37
Proportion of time in head shake	0.04	0.03	0.00 ; 0.09
Proportion of time in changeover	0.03	0.04	0.00 ; 0.14
Proportion of time in chick grooming	0.02	0.05	0.00 ; 0.21
Proportion of time in sky pointing	0.02	0.03	0.00 ; 0.11
Proportion of time in nape bite	0.01	0.03	0.00 ; 0.12
Proportion of time in chick feeding	<0.01	0.01	0.00 ; 0.05
Proportion of time in flapping	<0.01	0.01	0.00 ; 0.06
Proportion of time in neighbour fight	<0.01	<0.01	0.00 ; <0.01
Proportion of time in shaking	<0.01	<0.01	0.00 ; 0.02
Proportion of time in yawning	<0.01	<0.01	0.00 ; 0.01

731 † 0°, 90°, 180° and 270° corresponds to North, West, South and East of the colony.

732 * adapted for circular variables.

733 Table A5. List of the candidate models selected for the Bayesian model averaging after the ‘leaps and bounds’ and Occam’s window exclusion
 734 processes.

Model number	Chick grooming	Change over	Head shake	Scissor / Bowing	Nape bite	Mutual preening	Individual preening	Sky pointing	Posterior model probabilities, $\pi(M_k y_N)$	BIC
<i>Trip duration, 27 models were selected in total, cumulative posterior probability for the 5 best candidate models was 0.484</i>										
1				•					0.134	-8.78
2				•	•				0.103	-8.26
3			•	•					0.093	-8.05
4	•		•	•					0.091	-8.02
5			•	•	•				0.063	-7.27
<i>Posterior effect probabilities, $P(\beta \neq 0 y_N)$</i>	0.149	0.105	0.351	0.978	0.349	0.213	0.084	0.127		

Distance to the main foraging spot, 19 models were selected in total, cumulative posterior probability for the 5 best candidate models was 0.596

1			•			•	•		0.260	-59.06
2			•				•		0.129	-57.66
3			•	•			•		0.085	-56.82
4			•			•			0.064	-56.26
5			•	•					0.058	-56.06

Posterior effect 0.039 0.024 0.815 0.272 0.027 0.514 0.689 0.083

probabilities, $P(\beta \neq 0 | y_N)$

Direction to the main foraging spot, 19 models were selected in total, cumulative posterior probability for the 5 best candidate models was 0.803

1			•			•	•		0.331	-57.59
2			•				•		0.223	-56.81
3			•				•	•	0.089	-54.97
4			•	•			•		0.087	-54.93
5		•	•				•		0.073	-54.57

Posterior effect 0.073 0.047 0.907 0.087 0.058 0.363 1.000 0.107

probabilities, $P(\beta \neq 0 \mid y_N)$

735 NB: We only display the five best models for each BMA. For comparative purposes, BIC of the null model (without covariate) in the frame of
736 the BMA analysis was 0 for *Trip duration* model, -52.33 for *Distance to the main foraging spot* model, and -37.2 for *Direction to the main*
737 *foraging spot* model. The null model was not retained in the subset of candidate models in each BMA analysis.

738 Table A6. Relationship between total time of the dance ceremony in Cape gannet and their
 739 preceding foraging trip features, between 2013 and 2016 at Malgas Island, assessed with Cox
 740 proportional hazards models, with the parameters estimates (β), their standard errors (SE),
 741 their 95% confidence intervals (CI) and P -value adjusted with Benjamini-Yekutieli
 742 correction.

	β	SE	95% CI	Adjusted P -value
<i>Model 1, AIC = 126.12</i>				
Duration of foraging trip (h)	0.066	0.019	0.028 ; 0.104	<0.01
Test for the proportional hazard assumption: $\chi^2_{df=1} = 1.33, P = 0.25$				
<i>Model 2, AIC = 132.79</i>				
Distance to the main foraging spot (km)	0.012	0.005	0.002 ; 0.021	0.05
Test for the proportional hazard assumption: $\chi^2_{df=1} = 0.09, P = 0.76$				
<i>Model 3, AIC = 135.36</i>				
Direction to the main foraging spot ($^\circ$)	0.007	0.004	-0.002 ; 0.015	0.26
Test for the proportional hazard assumption: $\chi^2_{df=1} = 2.85, P = 0.09$				

743 NB: Three distinct models were fitted. The first two models had a deltaAIC >2 compared to a
 744 null model without covariate (AICnull model = 135.78).

745 Figure captions.

746

747 Figure 1. Cape gannet (*Morus capensis*) pair displaying 'scissors' to neighbours during its
748 dance ceremony, on Malgas Island (South Africa), November 2016 (Picture credit: D.
749 Grémillet).

750

751 Figure 2. Distribution of the 28 foraging trips of Cape gannets breeding in the Malgas Island
752 (South Africa), between 2013 and 2016. Red dots indicate the main foraging spot for each
753 trip. Map has been realized thanks to *marmap* (Pante & Simon-Bouhet, 2013) package for R
754 software (R Core Team, 2016).

755

756 Figure 3. Predicted total time of dance ceremony (in s, solid line) with its 95% confidence
757 interval (grey area) depending on (a) the duration of the previous foraging trip (in h) and (b)
758 the distance to the main foraging spot, for 28 Cape gannets breeding on Malgas Island (South
759 Africa), between 2013 and 2016, using Cox proportional hazards models. Raw data are shown
760 (black dot). Results presented in Fig. 3a are not sensitive to the extreme value with a foraging
761 trip duration ~80h.

762

763 Figure 4. Predicted relationship (solid line) between the features of dance ceremony and those
764 of the previous foraging trip for 28 Cape gannets breeding on Malgas Island (South Africa),
765 between 2013 and 2016. Values along the X-axis are back-transformed to facilitate
766 interpretation. In figure 4b, raw data (black dot) and the 95% interval for predictive estimates
767 (grey area) are shown, and 0°, 90° and 180° corresponds to North, West and South of the
768 colony, respectively.

769

770 Figure A1. Example of the result of the segmentation-clustering model for the foraging track
771 of the Cape gannet ID4 in 2016. We looked for the phases that are stationary in terms of the
772 smoothed speed in $\text{m}\cdot\text{h}^{-1}$ (i.e., speed smoothed over two steps before and after the focus
773 location) and the turning angle measured at constant step length in rad (i.e., angle between the
774 focus location, the first location entering a circle of radius equal to the median step length,
775 and the last location inside the circle). We considered that these phases corresponded to three
776 types of behavioural mode: transiting, feeding and resting, preliminarily composed of four
777 possible states to compensate the change in current velocity that can artificially produce
778 several different resting class. (a) In the example below, the states 1 and 2 correspond to the
779 resting phases (low speed and low variance in turning angle), the state 3 to the feeding phases
780 (moderate speed and high variance in turning angle) and the state 4 to the transiting phases
781 (high speed and low variance in turning angle). (b) We also showed the result of the
782 segmentation-clustering on a map.

783

784 Figure A2. Distributions of means (μ) and their standard deviations (SD) of the speeds and
785 turning angles measured at constant step length characterizing the resting, feeding or
786 transiting movement phases along 28 at sea foraging tracks of Cape gannets.

787

788 Figure A3. Correlation circles based on a principal component analysis including the three
789 foraging trip features and the 15 dance ceremony features used in our analyses. We showed
790 the correlation circle between the 1st and 2nd axes, the 1st and 3rd axes, and the 1st and 4th axes.
791 The length of the arrows corresponds to the \cos^2 value, a meaning of the qualitative
792 representation of the variables on the correlation circle. We used a colour coding to
793 distinguish between the dance duration (red), the dance displays (blue) and the foraging trip
794 features (green).







