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1 Impact of long-term behavioural studies in the wild: the blue petrel
2 (*Halobaena caerulea*) case at Kerguelen

3

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8

9 **Keywords:** behaviour, capture/recapture, human impact, long term studies, multi-
10 event model, seabirds

11

12 **Bullet points (85 characters max):**

13 - Experimental manipulations in wild animals may have an impact on future behaviour

14 - When possible capture/recapture studies on disturbed individuals should be
15 performed

16 - A new multi-event model to account for manipulations independently was developed

17 - Some species do not seem to suffer effects of manipulation

18

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21

22

23 Abstract

24 The study of animal behaviour contributes to understand how individuals or
25 populations live and survive. To this purpose researchers often manipulate, in a broad sense,
26 wild animals in sensitive periods, such as breeding, when animals are accessible/available.
27 However rare are those studies that show the impact of these manipulations on survival of
28 individuals. In this study we measured short and long term impact of experimental
29 manipulations on a small colony of blue petrels (*Halobaena caerulea*) at Kerguelen
30 archipelago where behavioural studies have been performed since 2006. We developed two
31 models to measure manipulation potential impacts, i) a new multi-event model that allows us
32 to account for different severity classes of experimental manipulations independently; ii) a
33 model that allows us to consider cumulative impact over years of these experimental
34 manipulations. Our results show that there is no evidence that our experimental manipulations
35 have negatively affected survival or breeding probabilities either in the short or in the long
36 term. Conversely, similarly to other studies on blue petrel's capture-recapture studies, the
37 survival was shown to be dependent on the bird experience (birds that reproduced seemingly
38 for the first time versus birds that already reproduced several times before), and the breeding
39 probability to be dependent on the year possibly because of environmental conditions.

40

41 Introduction

42 The study of animal behaviour allows researchers to understand why and how
43 individuals or populations live and survive in their natural environment. In the context of
44 climate change, understanding animal behaviour is crucial to understand how organisms adapt
45 themselves to a new/changing environment. However, researchers are often required to
46 manipulate wild animals to have an insight of a given behaviour (Gagliardo et al., 2013).
47 According to the species and the scientific quest, researchers establish precise protocols, take
48 individual measurements, and may also equip animals with specific devices. For instance,
49 scientists may use GPS or ARGOS transmitter to study movement and foraging strategy
50 (Weimerskirch, Le Corre, Jaquemet, & Marsac, 2005). In that context, a natural question is
51 how these manipulations broadly speaking may influence animal behaviours.

52 Wild animals are, very often, difficult to observe and so to capture, along the year. In
53 this context, most of studies are concentrated during specific periods of the day (alimentation
54 period) or seasons of the year (breeding or migration period). In those periods, animals form
55 large groups, and come back every day or year to the same place to feed, breed, rest, or
56 winter. So, replicable observations, experiments, and long-term studies are possible. The
57 breeding season is the longest period in terms of time and the only possible moment to study
58 some species such as sea-animals (Wallace et al., 2007). Breeding period also allows to study
59 a component of individual fitness of animals through the study of offspring production
60 (Kolliker, Brodie, & Moore, 2005). However, breeding is also very challenging for wild
61 animals. Indeed, it corresponds to the moment where individuals invest the most of their
62 energy to find a mate and to raise their youngs, and all kind of manipulations may have an
63 effect on breeding and survival. In addition of “natural” energy expended to survive or to take
64 care of offspring, researchers’ proximity, interactions, and manipulations may influence
65 behaviour, physiology and eventually long-term survival and fitness of animals, adding
66 supplementary costs in their energy allocation. In this context, a better understanding of the
67 potential impact of manipulations (especially negative impacts) on studied animals is essential
68 both for the sake of an ethical work, and for the estimation of the introduced biases in the data
69 collected. In recent scientific literature, several studies tried to understand capture and
70 marking impacts on animals at individual and population levels (Parris et al., 2010; Wilson &
71 McMahan, 2006). For example, Stien & Ims (2016), showed substantial research impact on
72 birds. They compared their Common Eiders’ (*Somateria mollissima*) studied colony with a
73 less disturbed colony of the same species, and highlighted that manipulation in the studied
74 colony increased nest failure from predation.

75 Weimerskirch and colleagues (2002) have shown that the stress induced by human
76 proximity, capture, and handling is unavoidable and may lead sometimes to a decrease in

77 breeding probability, and survival (see also Sapolsky, Romero, & Munck, 2000). In addition
78 of stress, capture and handling may also lead to injury or death. Physical marking as toe-
79 clipping (small mammals and amphibians) and hot-iron branding (pinnipeds) can expose
80 tissue to infection (Green & Bradshaw, 2004; Perry, Wallace, Perry, Curzer, & Muhlberger,
81 2011) and external attachment such as ring (birds, bats) can cause tissue compression (Baker
82 et al., 2001). In the last decade, electronics devices (i.e. loggers and/or satellite transmitters)
83 were used to study free ranging individuals mainly during migration or foraging. However,
84 and especially for birds, the energy required for migration or foraging can be increased by
85 these devices due to weight, size, air/water drag, and devices' position on the animal (Barron,
86 Brawn, & Weatherhead, 2010; Y. Ropert-Coudert, Knott, Chiaradia, & Kato, 2007). Studies
87 on potential impacts of capture and marking techniques on seabirds are numerous (Ackerman
88 et al., 2004; Y Ropert-Coudert et al., 2000; Saraux et al., 2011). For example, in sooty
89 shearwaters (*Puffinus griseus*), a procellariiforms species, breeding pairs who were captured
90 and equipped with tags during the breeding season were more likely to desert their nests than
91 non-captured pairs (Adams et al., 2009).

92 Behavioural studies are often repeated over years in the same colony during the same
93 period, but their long-term potential impacts are rarely clearly detailed and to our knowledge
94 there are no such impact studies on classical behavioural protocols applied to wild animals.
95 Most of the impact studies cited above focalised on the effect of a specific device/technique,
96 or considered the general impact of human disturbing due to a long term study in a colony.
97 However, behavioural studies are often “one shoot” on few individuals, and manipulated
98 animals are at best followed in their fate in the same year of the experiment. Long term effects
99 of manipulations are thus unknown. In this context, it seems interesting to study the potential
100 impacts of long-term behavioural experiments on survival and on probability of breeding of a
101 given population/colony/individuals. This may be possible only if the studied animals are
102 followed individually over years, accurately noting all the manipulations to which each
103 individual underwent. In this case, a capture-recapture (CR) approach (Lebreton, Burnham,
104 Clobert, & Anderson, 1992) would be possible.

105 For our study, we used the data from a long-term behavioural study focused on
106 behaviour (mainly orientation mechanisms and communication among individuals) of blue
107 petrels (*Halobaena caerulea*) during the incubation period in Kerguelen archipelago (southern
108 Indian Ocean). From the beginning of the long-term study in 2006 researchers noted which
109 individual bird participated in a given experiment, and all birds were followed along the study
110 period checking their presence, absence, and breeding each year. We used classical CR
111 approach and adapted it to our dataset and our field-work protocols. Consequently, a new

112 model belonging to the class of multi-event CR models (R. Pradel, 2005) was developed to
113 test potential impacts from experimental manipulations.

114 The first objective of this study is to establish the impact of different type of
115 experimental manipulations on survival and probability to breed the year following the
116 experimental manipulation (hereafter called simply “next year”) of breeding blue petrels. Due
117 to the large variability of the experimental manipulations it is difficult to predict any
118 hierarchy, but we expect that manipulated individuals will have a lower survival and
119 probability to breed next year than non-manipulated individuals. The second objective is to
120 study a potential cumulative impact of experimental manipulations. We thought that even if
121 we detect no impact of experimental manipulations on these blue petrels when they are
122 manipulated during only one season, it is possible that a cumulative impact exists if they are
123 manipulated several years in a row. In penguins, for instance, the decrease of survival and
124 reproductive success of banded individuals compared to unbanded individuals was not
125 observed during the first year after banding but after several years (Gauthier-Clerc et al.,
126 2004; Saraux et al., 2011). In this context, we expect that survival and breeding probabilities
127 will decrease with the increase of the number of manipulations in a row. Previous studies on
128 blue petrels have shown that survival and breeding probabilities are conditional on the
129 breeding experience. Indeed, experienced breeders had a higher survival and probability to
130 breed next year than inexperienced one (Barbraud & Weimerskirch, 2005; Chastel,
131 Weimerskirch, & Jouventin, 1995). In addition, studies have shown that probability to breed
132 in blue petrels was variable over time and dependent on environmental conditions (Barbraud
133 & Weimerskirch, 2003). From these studies we predict that survival and breeding probability
134 next year will be higher for those pairs that bred the years before than those pairs that are
135 found for the first time in the colony.

136

137 Methods

138 *Species and study area*

139 The study was conducted on Verte Island (49°51'S, 70°05'E) in the Kerguelen
140 archipelago, southern Indian Ocean between 2006 and 2016. The blue petrels of a small
141 colony were used during incubation period to perform behavioural experiments (i.e. Y-maze
142 binary choice experiments), and collect different samples (i.e. blood, feathers, and uropygial
143 gland's secretions) for studying olfactory communication (all hereafter called simply
144 experimental manipulations). Blue petrels are small (190g) long-lived seabird from southern
145 hemisphere belonging to procellariiforms order. At mid-October, they come back on land
146 annually to breed in the same colony, laying a unique egg in an underground nest (burrow).

147 Both parents incubate the egg with a similar investment and incubation lasts about 51 days
148 (Brooke, 2004). These birds are known mostly to use their own burrow over years and they
149 are lifelong socially and genetically faithful to the mate (Bried & Jouventin 2002; Bried,
150 Pontier, & Jouventin 2003). Over the study period, each year, approximately one hundred
151 burrows were checked in November to list occupied burrows. During the field work season
152 (November to December) the burrows were regularly checked to identify both mates breeding
153 in it, and to perform experimental manipulations on these individuals. When a non-ringed bird
154 was found, it was ringed, weighted and morphological measures taken (first capture). When a
155 bird was already ringed, only the ring number was controlled, and bird weighted (re-sighting).
156 Individuals warming an egg were considered as breeders and individuals who were never
157 found with an egg were considered as non-breeders. Since 2006, 501 individuals were
158 individually marked and followed.

159 Rarely at the first capture, but regularly from first re-sighting, blue petrels were
160 randomly assigned by the experimenters to different experimental manipulations; these
161 occurred during the breeding period, between November and hatching in mid-end December.
162 In this context, each year, each breeding individual bird was assigned to one unique type of
163 experimental manipulation. For each field season, a fixed number of individuals was
164 randomly assigned to each experimental manipulation. Some re-sighted individuals remained
165 also not used for experimental manipulations and became reference individuals. If possible,
166 we avoided to use birds over 2 consecutive years. In many cases, however, either it was not
167 possible i) because of the low number of pairs breeding at the colony and the number of birds
168 needed for the experiments, or alternatively ii) because our protocols were exactly to sample
169 birds over consecutive years to assess, for instance, variation of the own odour (e.g. Mardon et
170 al. 2010). It is useful to remember here that the goal of our research program was to study
171 behaviour. Due to the probable variations of potential stress induced in individual birds by
172 different experimental manipulations, we chose to categorize them in four severity classes
173 (Table 1). This categorisation is based on our personal experience/knowledge of wild birds
174 ecology/behaviour/reactions, and are not linked to severity degrees commonly used in animal
175 experimentation as those are largely based on lab mammals behaviour.

176

177

178 *Ethical Note*

179 All experimental manipulations cited and performed since 2006 were approved by
180 French Ethical Committee after favourable recommendation of Comité d’Ethique pour
181 L’Expérimentation Animale Languedoc-Roussillon (CEEA-LR), C2EA n°36, by the Ethical

182 Committee of Institut Polaire Français Paul Emile Victor (IPEV), and by the Ethical
183 Committee of Reserve Naturelle des Terres Australes et Antarctiques Françaises (TAAF).

184

185 *Model 1: Effect of manipulations*

186 To account for a potential impact of the four severity classes of experimental
187 manipulations on birds from the colony, we analysed the data with multi-event CR models (R.
188 Pradel, 2005). Models were built using three kinds of parameters: the initial states
189 probabilities, the transition probabilities and the event probabilities. To account for
190 experimental manipulations' impacts, we had to adapt classical capture-recapture models.
191 Because being manipulated was conditional of being caught, the capture process was included
192 in the transition process before the manipulation process. Models were based on a diagram of
193 fate defined by the Fig.1 and so, transition probabilities were defined by a four steps
194 formulation involving: the survival probability, Φ , the breeding probability conditional on
195 survival, Ψ , the capture probability, p , and finally the experimentation probability conditional
196 on capture, e (see model 1 in Appendix Fig. A1, transition probabilities). In this model, there
197 are nine possible states that change over time according to a Markov process and seven
198 possible events that are generated from the states on each occasion (Fig.1). Because capture is
199 modelled in transition probability, then, event probabilities were degenerated and fixed to 1
200 (see model 1 in Appendix Fig. A1, event probabilities). We used program E-SURGE 2.2 (R
201 Choquet, Rouan, & Pradel, 2009) for parameter estimation and model.

202 Goodness-of-fit (GOF) tests for multistate model were performed with program U-
203 CARE 2.3.4 (R. Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). These tests were
204 based on the JollyMove model (Brownie *et al.*, 1993) with the assumptions that survival,
205 transition between states and encounter probabilities were homogeneous among individuals
206 (R Pradel, Gimenez, & Lebreton, 2005). The separation in four severity classes of
207 experimental manipulations may lead to a potential lack of data to do the GOF tests. In this
208 context, we choose to test for overdispersion by gathering all manipulated individual in only
209 one class. Model selection was based on the Akaike's Information Criterion (AIC; Akaike,
210 1987) adjusted for small sample size and overdispersion (QAICc; R Choquet *et al.*, 2009).
211 We have considered two models significantly different when their QAICc differed by more
212 than 2 units (Burnham & Anderson, 2002). If two models were separated by less than two
213 units we chose the simplest one.

214 To understand the potential impacts of the different severity classes of experimental
215 manipulations, we tested four effects: the severity effect, the manipulated effect, the breeder
216 effect and the three classes of manipulations effect. In the first case, estimations were set

217 different between all severity classes of experimental manipulations. So, this effect (hereafter
218 called “*severity*”) has four levels, one for each class of experimental manipulations of severity
219 and one level of no manipulation. In the second case (hereafter called “*manipulated*”), we
220 differentiated not manipulated breeders and manipulated breeders. For the third effect
221 (hereafter written “*breeder*”) there are two levels, one for each breeding status. In the fourth
222 case (hereafter called “*three classes of manipulations*”), we set together levels two and three
223 of the “*severity effect*”, as the manipulation included in these two classes were quite similar.
224 Each states effect and a time effect were tested independently. We also tested for a potential
225 transience effect (effect which differentiates the survival after first capture from the next
226 survival R. Pradel, Cooch, & Cooke, 1995). Transient individuals were shown to be present in
227 previous studies on blue petrels (Barbraud & Weimerskirch, 2005; Chastel et al., 1995).
228 Indeed, these studies showed that inexperienced breeders had a lower survival than
229 experienced breeders and that could come from permanent emigration of individuals caught
230 for the first time (inexperienced breeders). In this study, we used a proxy: based on our
231 protocol, breeders captured for the first-time may correspond to inexperienced breeders
232 whereas a recaptured individual has very small probabilities to be an inexperienced breeder.
233 Concerning the sex effect, a preliminary analysis showed no differences between males and
234 females for both survival and probability to breed next year. Based on this pre-analysis we
235 pooled together males and females. We used a general model with a severity effect in
236 interaction with a time effect on each probability. In addition, a two age effect was applied on
237 survival to begin the model selection. The umbrella model is Φ (*transience x time x severity*),
238 Ψ (*time x severity*), p (*time x severity*), e (*time x severity*). Then a four-step analysis was
239 used: we determined the best effect according to QAICc for experiment probability (e)
240 starting from the umbrella model. Second, the best effect for capture probability (p) was
241 determined starting from the best model of step 1. Third, the best effect for breeding
242 probability (Ψ) was determined starting from the model retained in the step. Fourth, the best
243 effect for survival probability (Φ) was determined starting from the model retained in the step
244 fourth. In total, we fitted 39 models and selected the best model according to QAICc.

245

246 *Model 2: Cumulative effect of manipulations*

247 With the first model, we tested for a one-year effect of experimental manipulations on
248 survival and reproduction. However, experimental manipulations may have a long-term
249 impact. Therefore, we tested for a potential cumulative effect of the experimental
250 manipulations over years to understand how experiments may impact an individual when it is
251 manipulated several years in a row.

252 We used the same dataset of 501 individuals as in the first model except that all experimental
253 manipulations were gathered in one class. The general approach was similar to the first model
254 except that survival, breeding and capture probabilities at time t might be conditional to have
255 been already manipulated at least two times in a row. In this second model we consider nine
256 states: ‘alive non-breeder not caught’, ‘alive non-breeder and caught’, ‘alive breeder and not
257 caught’, ‘alive as breeder’, ‘caught and not manipulated’, ‘alive as breeder’, ‘manipulated the
258 last year but not caught’, ‘alive as breeder’, ‘caught and manipulated one year’, ‘alive as
259 breeder’, ‘manipulated two years in a row but not caught’, ‘alive as breeder’, ‘caught and
260 manipulated two or more years in a row’ and ‘dead’ (Fig. 2). Four possible events are
261 recorded: ‘not observable’, ‘non-breeder’, ‘breeder non-manipulated’, ‘breeder manipulated’.
262 Consequently, models were based on a new diagram of fate with specific transition between
263 states, defined in Fig. 2. Transition probabilities were characterized by four steps: the survival
264 probability, Φ , the breeding probability conditional on survival, Ψ , the capture probability, p ,
265 and finally a new parameter movement probability (probability of changing the status of
266 manipulation), m , conditional on capture which increment or not the status of the
267 experimental manipulation (see model 2 in Appendix Fig. A2, transition probabilities). Event
268 probabilities were degenerated and fixed to one (see model 2 in Appendix Fig. A2, event
269 probabilities).

270 To understand the long-term effect of experimental manipulations we tested three
271 main effects: the cumulative effect, the manipulated effect and the breeder effect. The
272 *cumulative* effect has three levels, “not manipulated”, “be manipulated one year only” or “two
273 or more years in a row”. The “manipulated” and “breeder” effects are defined as in Model 1.
274 We tested independently each states association but also a potential time effect on each
275 probability and a transient effect on survival probabilities. We used a general model with a
276 cumulative effect in interaction with a time effect on each probability to begin the model
277 selection. The umbrella model is Φ (*transience x time x cumulative*), Ψ (*time x cumulative*), p
278 (*time x cumulative*), e (*time x cumulative*). As for model 1, we followed a four-step analysis.
279 We determined the best effect according to QAICc for movement probability (m) starting
280 from the umbrella model. Second, the best effect for capture probability (p) was determined
281 starting from the best model of step 1. Third, the best effect for breeding probability (Ψ) was
282 determined starting from the model retained in the step. Fourth, the best effect for survival
283 probability (Φ) was determined starting from the model retained in the step fourth. In total,
284 we fitted 37 models and selected the best model according to QAICc.

285

286 Results

287 *Model 1: Effect of manipulations*

288 The GOF tests for model 1 showed no overdispersion (Appendix Table A1), so, the
289 default value is fixed for the variance inflation factor ($\hat{c} = 1$). The test of transience is very
290 close to be significant (p -value = 0.051). As we said earlier, different studies showed that a
291 transient effect exists on other blue petrels' colonies, so we tested for this effect on survival
292 probabilities.

293 Model selection is summarized in Appendix Table A2. According to QAICc the best
294 model suggested a potential three classes of experimental manipulations effect in addition of a
295 transient effect on survival probabilities, a time and a breeder effect for breeding probabilities,
296 a time and a manipulated effect on capture probabilities and a time and severity effect on
297 experiment probabilities. However, estimates show that there is no evidence that
298 manipulations have a negative effect on survival. In fact, for already known individuals (Fig.
299 3c), the survival of non-manipulate birds (0.86, s.e. = 0.02) was lower than second and third
300 severity classes manipulated birds (0.93, s.e. = 0.03) but higher than individual in the first
301 class of experimental manipulation (0.82, s.e. = 0.04) with large confidence intervals. The
302 estimate of survival for the last class of experimental manipulations was lower than every
303 other estimate with even larger confidence intervals (0.71, s.e. = 0.08). Probabilities to breed
304 the next year were similar between non-manipulated and manipulated individuals and variable
305 over time. These estimations were higher (between 0.80 and 1.0) for individual who bred
306 between 2006 and 2008 and in 2014 and lowest in 2013 (Fig. 3a). This rate was not estimable
307 in 2012 probably due to the absence of experimental manipulations during this year. As
308 expected, the transient effect was retained on the best model, and it showed that survival of
309 individual caught for the first time (apparent survival) was lower than the survival of
310 individuals already caught (Fig. 3b et c).

311

312 *Model 2: Cumulative effect of manipulations*

313 Model selection is summarized Appendix Table A3. According to QAICc the best
314 model showed a breeder effect and a transient effect on survival probabilities, a time and a
315 breeder effect for breeding probabilities, a time effect on capture probabilities and a time in
316 addition of a cumulative effect on movement probabilities. The best model showed a breeder
317 effect on both survival and breeding. Probabilities to breed the next year were higher
318 (between 0.80 and 1.0) for individuals who bred between 2006 and 2009, 2014 and 2015.
319 This rate was lowest in 2013 and not estimable in 2012 (Fig. 4a). As for the first model,
320 model with a transient effect on survival probabilities is the best model. It showed that

321 survival of individuals caught for the first time was lower than the survival of already caught
322 individuals. A model, close to the best model, where cumulative effect is studied, showed
323 similar estimates between non-manipulated individuals (0.87, s.e. = 0.02), individuals
324 manipulated one year (0.85, s.e. = 0.03), and individuals manipulated two or more years in a
325 row (0.88, s.e. = 0.03; Fig. 4b and c).

326

327 Discussion

328 We measured short and long term impact of experimental manipulations on a small
329 colony of blue petrels. To that purpose, we first developed a new multi-event model that
330 allowed us to account for different severity classes of experimental manipulations and to
331 measure their potential impacts independently. Secondly, we developed a model that allowed
332 us to consider cumulative impact over years of these experimental manipulations. Applying
333 those models to our blue petrels' data set, contrarily to our predictions, we found no evidence
334 that the experimental manipulations performed have short or long term impact on both
335 survival and breeding probabilities. In addition, similarly to other studies on undisturbed blue
336 petrels, the survival was shown to be dependent on the bird experience and the breeding
337 probability to be dependent on time (Barbraud & Weimerskirch, 2003, 2005; Chastel et al.,
338 1995).

339

340 *Effect of experimental manipulations on survival*

341 In blue petrels' colony of our study, the first model showed that survival probabilities
342 were almost similar between non-manipulated individuals and manipulated individuals with
343 confidence intervals that largely overlapped. If we examine precisely estimates, the
344 probability to survive of birds used for behavioural experiments (table 1; figure 3) was
345 slightly lower than non-manipulated individuals and individuals manipulated with sampling
346 experiments had a slightly higher probability to survive than non-manipulated individuals.
347 Individuals manipulated in the fourth-severity class of experimental manipulations have the
348 lowest survival estimate. Due to the confidence intervals, it is impossible to conclude for a
349 negative impact of the fourth-severity class of experimental manipulations, however. In
350 addition, the second model highlights that survival probability is similar between all breeders'
351 individuals in the colony independently of whether they were manipulated or not. Both the
352 first and the second model showed that survival probabilities in this population stay over 0.80
353 and may be considered as high and, comparable to estimates of undisturbed blue petrels from

354 another colony (Barbraud & Weimerskirch, 2005) but also in other seabirds' species (Cam &
355 Monnat, 2000; Le Bohec et al., 2007).

356 As we predicted, survival probabilities of first-time caught individuals were lower than
357 for already caught individuals. A well described phenomenon for different procellariiforms
358 species is the so called skipping behaviour (Converse, Kendall, Doherty, & Ryan, 2009; Sanz-
359 Aguilar et al., 2011). Individuals can be absent from the colony during one season, and
360 consequently their burrows are empty and new inexperienced individuals could take place
361 into it for that season (Bonadonna & Mardon, 2010). However, the following year, the current
362 owners of the burrow could come back and occupy their place and squatters must find another
363 place. Consequently, the potential explanation of our result may be that first-time caught
364 individuals manipulated were squatters that moved elsewhere in subsequent years and were
365 not found again.

366 *Effect of experimental manipulations on breeding*

367 Breeding blue petrels, manipulated or not, had the same probability, conditional to
368 survive, to breed again the next year. This result may suggest that manipulations don't affect
369 the breeding status next year. Nevertheless, as we predicted, variation temporal effect was
370 retained by model selection. For example, the lowest probability to breed the next year was
371 estimated for individual that bred in 2013. Interestingly, in 2014, environmental conditions
372 were globally unfavourable and only few nests (less than 20) were occupied. Thus, it is
373 possible that a large part of individuals that bred in 2013 may have skipped the breeding
374 season in 2014. In this study, we showed that breeding probabilities are potentially impacted
375 by environmental conditions, but potentially not by manipulations. In this context, a
376 cumulative effect of manipulations with potentially bad environmental conditions couldn't be
377 showed. The winter period for blue petrel is crucial, most of mortality occurs between
378 breeding periods and warm sea-surface, due to climate variations, can negatively impact
379 breeding probability (Barbraud & Weimerskirch, 2003; Guinet, Chastel, Koudil, Durbec, &
380 Jouventin, 1998). On a larger scale, several studies showed an important impact of climate
381 variations on breeding probability for other species of procellariiforms but also, more
382 generally in seabirds (Barbraud et al., 2011; Croxall, Trathan, & Murphy, 2002; Jenouvrier,
383 Barbraud, & Weimerskirch, 2005).

384

385 *Perspectives*

386 Research on wild populations, especially behavioural experiments that required
387 animals' manipulations, leads to ethical questions. For the sake of an ethical work, an analysis

388 of the potential impacts on wild animals, when it is possible, is essential. In addition of
389 important information about the researchers' impact on studied animals, this kind of analysis
390 is important to guaranty the quality and trustworthiness of the data collected during both short
391 and long-term studies. Finally, in case of impact, finding out which aspect of the population
392 (e.g. breeding, survival, age range etc.) are affected may help to modify protocols, act to
393 reverse this negative impact, and obtain trustworthy data according to scientific hypotheses
394 that one would like to test.

395 In this study, we have developed a new model of multi-event capture-recapture to
396 understand the potential impact of behavioural experiments that occurs for 11 years on a small
397 blue petrels' colony. This model has proved its usefulness to study experimental
398 manipulations impacts on survival and breeding probabilities next year but also its capacity to
399 detect already known phenomena about blue petrels. Then, our approach should be developed
400 and used for other species of birds, mammals or amphibian when they are captured directly in
401 their nest or burrow and followed during long and repeated period. The development of this
402 kind of studies may help to understand all the impacts that researchers may have on wild
403 populations from any kind of manipulations, experiments and sampling in addition of capture
404 and marking. In this context, when all requirements are filled, our approach may become a
405 new ethical critical step that each study will might have to follow.

406

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414

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Table1: Description of the different severity classes

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Severity classes	Time in hands (min)	Type of experiments	Example of experimental manipulations
1st class	< 5	Behavioural	Head-space sampling, Y-maze experiments, short distance homing
2nd class	5 to 15	Sampling	Blood sampling, odour collection by cotton swab
3rd class	15 to 30	Samplings in a row	Blood, feather and uropygial secretions sampling and cloacal and oral smear
4th class	15 to 30	Different experiments and samplings	Repeated feathers and secretions sampling, antibiotic injection with repeated blood sampling, electrocardiogram

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577 Classes were decided according to manipulation time, the type and number of experimental manipulations. Few
578 examples are given. (Experimental manipulations are precisely described in: Bonadonna, Caro, Jouventin, &
579 Nevitt, 2006; Bonadonna & Mardon, 2010; Bonadonna, Villafane, Bajzak, & Jouventin 2004; Gabirot et al.,
580 2016; Leclaire, Bourret, & Bonadonna, 2017; Leclaire, Strandh, Mardon, Westerdahl, & Bonadonna, 2017; J
581 Mardon & Bonadonna, 2009; J Mardon, Saunders, & Bonadonna, 2011; J. Mardon, Saunders, Anderson,
582 Couchoux, & Bonadonna, 2010; Strandh et al., 2012).

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585 **Appendix tables**

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Table A1: Goodness-of-fit tests of the JollyMove model (JMV model) obtained with U-CARE software when all the severity classes are gathering.

Goodness-of-fit components	χ^2	p-value	df
Test WBWA	10.44	0.941	19
Test 3G.SR	33.842	0.051	22
Test 3G.SM	37.642	0.999	70
Test M.ITEC	8.803	0.267	7
Test MLTEC	3.269	0.514	4

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Test WBWA: where before where after (test of memory); test 3G.SR: test of transience; test 3G.SM: composite test (newly marked differed from previously marked birds as to when they are resighted); test M: if birds are more or less likely to be seen at the next occasion (M.ITEC) or subsequent ones (M.LTEC) compare to when they are not seen. df =degree of freedom.

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Table A2: List of models tested for potential differences between the four different manipulations severity classes.

Parameters	Effects	Number of estimated parameters	Deviance	QAICc	Codes	
Step 1:	time x severity	188	4205.52	4656.64	1	
Experiment, <i>e</i>	time	176	4725.96	5142.99	2	
	severity	170	4828.40	5228.71	3	
	time + severity	179	4577.51	5002.99	4	
Step 2:	time x severity	188	4205.52	4656.64	5	
Capture, <i>p</i>	time	172	4296.16	4702.03	6	
	severity	170	4283.24	4683.56	7	
	breeder	169	4284.51	4682.05	8	
	manipulated	167	4287.33	4679.36	9	
	three classes of manipulations	170	4282.23	4682.54	10	
	manipulated + time	174	4248.18	4659.62	11	
	manipulated x time	183	4213.97	4650.79	12	
	time x severity	183	4213.97	4650.79	13	
Step 3:	time x severity	183	4213.97	4650.79	13	
Breeding, Ψ	time	151	4284.62	4633.32	14	
	severity	160	4275.92	4648.81	15	
	breeder	156	4282.04	4644.13	16	
	manipulated	157	4277.33	4642.11	17	
	three classes of manipulations	159	4276.01	4646.19	18	
	time + severity	165	4256.93	4643.46	19	
	time x breeder	169	4236.87	4634.42	20	
	time + breeder	161	4272.44	4648.05	21	
	time x manipulated	175	4229.69	4643.92	22	
	time + manipulated	162	4267.99	4646.32	23	
	time x three classes of manipulations	179	4222.57	4648.04	24	
	time + three classes of manipulations	164	4258.32	4642.11	25	
	Step 4:	time x severity x transience	169	4236.87	4634.42	26
	Survival, Φ	time x transience	121	4307.30	4578.45	27
severity x transience		115	4306.31	4562.49	28	
breeder x transience		107	4329.68	4566.19	29	
manipulated x transience		109	4322.43	4563.83	30	
[three classes of manipulations + time] x transience		146	4269.36	4604.80	31	
three classes of manipulations x time x transience		159	4273.43	4643.61	32	
three classes of manipulations + transience		109	4315.96	4557.36	33	
three classes of manipulations x transience		113	4311.56	4562.80	34	
three classes of manipulations + transience ⁽¹⁴⁾		98	4359.31	4574.04	35	
three classes of manipulations + transience ⁽¹⁴⁾		101	4355.53	4577.48	36	
manipulated x transience ⁽¹⁴⁾		97	4370.46	4582.80	37	
breeder x transience ⁽¹⁴⁾		95	4372.53	4580.08	38	
manipulated x transience ⁽¹⁴⁾	103	4350.60	4577.37	39		

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Appear: the number of estimated parameters, the deviance and the QAICc for each parameter. Best models for each parameter are in bold. Model selection began with a general model with severity and time effect on each parameter. Then, the best structure for Experiment (*e*) were determined with a time and a severity effect on Capture (*p*), Breeding (Ψ) and Survival (Φ). The best structure for *p* were determined with the best structure for *e*, a time and a severity effect on Ψ and Φ . The best structure for Ψ were determined with the best structure for *e* and *p* and a time and a severity effect on Φ . The best structure for Φ were determined with the best structure for *e*, *p* and Ψ . In step 3, two models were retained (Codes 14 and 20) but in step 4, models derived from model 14 perform badly (with a subscript (14)).

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Parameters	Effects	Number of estimable parameters	Deviance	QAICc	Codes
Step 1:	time x cumulative	157	3809.14	4173.92	1
Movement, <i>m</i>	time	143	3865.94	4193.50	2
	cumulative	136	4079.17	4388.51	3
	manipulated	135	4084.60	4391.35	4
	time + cumulative	146	3815.98	4148.79	5
	time x manipulated	151	3817.37	4166.07	6
	time + manipulated	144	3826.86	4157.04	7
	Step 2:	time x cumulative	146	3815.98	4148.79
Capture, <i>p</i>	time	124	3904.38	4183.07	9
	cumulative	119	3903.02	4169.15	10
	breeder	117	3914.36	4175.51	11
	manipulated	118	3903.30	4166.94	12
	manipulated + time	126	3870.85	4154.60	13
	manipulated x time	138	3825.20	4139.72	14
	Step 3:	time x cumulative	138	3825.20	4139.72
Breeding, Ψ	time	111	3892.30	4138.60	16
	cumulative	109	3886.24	4127.64	17
	breeder	107	3891.25	4127.76	18
	manipulated	108	3887.29	4126.24	19
	time + cumulative	114	3875.04	4128.74	20
	time x breeder	121	3847.79	4118.93	21
	time + breeder	112	3879.36	4128.13	22
	time x manipulated	129	3838.71	4130.09	23
	time + manipulated	113	3875.80	4127.03	24
	Step 4:	time x cumulative x transience	121	3847.79	4118.93
Survival, Φ	time x transience	82	3886.09	4063.03	26
	time + transience	75	3901.31	4062.07	27
	breeder + transience	67	3902.72	4045.26	28
	breeder x transience	68	3900.72	4045.52	29
	breeder x transience x time	94	3867.61	4072.78	30
	manipulated x transience	70	3900.60	4049.94	31
	manipulated + transience	68	3907.40	4052.20	32
	[time + cumulative] x transience	88	3875.23	4066.20	33
	[time + cumulative] + transience	78	3894.44	4062.11	34
	[time x cumulative] + transience	103	3869.16	4095.94	35
	cumulative + transience	69	3901.19	4048.26	36
cumulative x transience	71	3898.59	4050.21	37	

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612 Appear: the number of estimated parameters, the deviance and the QAICc for each parameter. Best models for
613 each parameter are in bold. Model selection began with a general model with cumulative and time effect on each
614 parameter. Then, the best structure for Movement (*m*) were determined with a time and a cumulative effect on
615 Capture (*p*), Breeding (Ψ) and Survival (Φ). The best structure for *p* were determined with the best structure for
616 *m*, a time and a cumulative effect on Ψ and Φ . The best structure for Ψ were determined with the best structure
617 for *m* and *p* and a time and a cumulative effect on Φ . The best structure for Φ were determined with the best
618 structure for *m*, *p* and Ψ .

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622 **Figure legends**

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625 Figure 1: Diagram of fate of adult blue petrels followed at Verte Island, Kerguelen archipelago during the
626 breeding season t until season t+1. Individuals start in states 1 to 8 at the extreme left of the diagram. The
627 transition probabilities are survival probability, Φ , breeding probability, Ψ , capture probability, p, and
628 experimentation probability, e. For each life history possibility, the state and the event associate are described. In
629 the table, states codes are associated with the states names.

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632 Figure 2: Diagram of fate of adult blue petrels followed at Verte Island, Kerguelen archipelago during the
633 breeding season t until season t+1 for cumulative effect of manipulations. Individuals start in states 1 to 8 at the
634 extreme left of the diagram. The transition probabilities are survival probability, Φ , breeding probability, Ψ ,
635 capture probability, p, and movement probability, m. For each life history possibility, the state and the event
636 associate are described. In the table, states codes are associated with the states names.

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639 Figure 3: (a) Probability of breeding the next year for all breeders (manipulated and not manipulated combine)
640 and survival probability according to state and capture: (b) first capture, (c) subsequent captures, in the blue
641 petrel colony at Verte Island, Kerguelen archipelago. \diamond for non-manipulate breeder, Δ for first class manipulate
642 breeders, ∇ for second and third class manipulate breeders, \times for fourth class manipulate breeders. Solid lines
643 represent the upper and lower confidence intervals (95%).

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646 Figure 4: (a) Probability of breeding the next year for all breeders (manipulated and not manipulated combine)
647 and survival probability according to state and capture: (b) first capture, (c) subsequent captures, in the blue
648 petrel colony at Verte Island, Kerguelen archipelago. Δ for non-manipulate breeder, ∇ for breeders manipulated
649 only one year, \times for breeders manipulated two or more years in a row. Solid lines represent the upper and lower
650 confidence intervals (95%).

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652 **Appendix figure legends**

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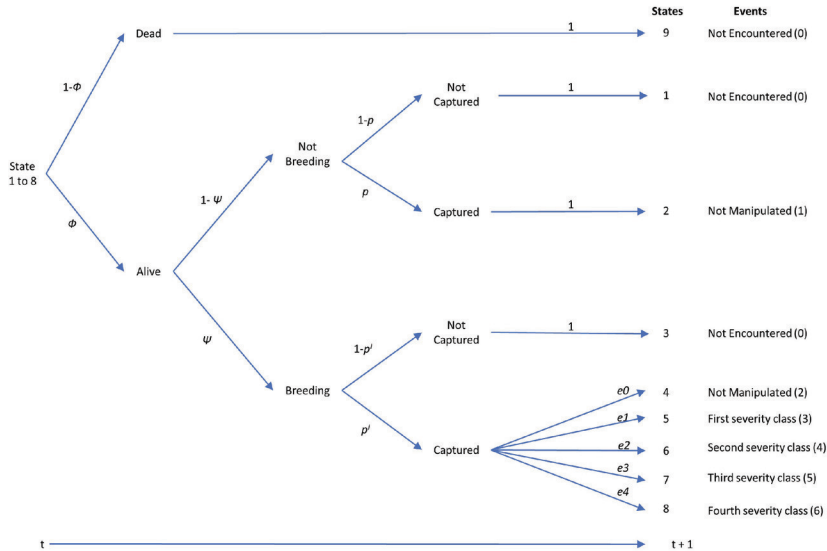
654 Figure A1: Model 1 implemented in E-SURGE; the model is a multi-event model. The
655 matrices are Markovian and are used to study the potential effect of the different severity
656 classes of manipulations on the blue petrel colony. Transition probabilities are separated in
657 four matrices corresponding to each part of an animal life history in our model.

658

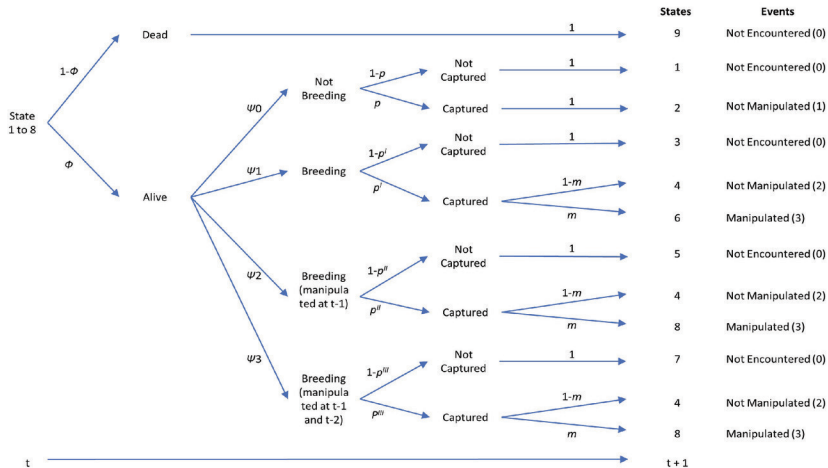
659

660 Figure A2: Model 2 implemented in E-SURGE; the model is a multi-event model. The
661 matrices are Markovian and are used to study the potential cumulative effect of manipulations
662 on the blue petrel colony. Transition probabilities are separated in four matrices
663 corresponding to each part of an animal life history in our model.

664



Codes	States of individuals
1	Alive as non-breeder and not caught
2	Alive as non-breeder and caught
3	Alive as breeder and not caught
4	Alive as breeder and caught and not manipulated
5	Alive as breeder, caught and manipulated with first severity class experimental manipulations
6	Alive as breeder, caught and manipulated with second severity class experimental manipulations
7	Alive as breeder, caught and manipulated with third severity class experimental manipulations
8	Alive as breeder, caught and manipulated with fourth severity class experimental manipulations
9	Dead



Codes	States of individuals
1	Alive as non-breeder but not caught
2	Alive as non-breeder and caught
3	Alive as breeder and not caught
4	Alive as breeder and caught and not manipulated
5	Alive as breeder, manipulated the last year but not caught
6	Alive as breeder, caught and manipulated one year
7	Alive as breeder, manipulated two years in a row but not caught
8	Alive as breeder, caught and manipulated two or more years in a row
9	Dead

