



**HAL**  
open science

## Impact of long-term behavioural studies in the wild: the blue petrel, *Halobaena caerulea*, case at Kerguelen

Matthieu Berges, Rémi Choquet, Francesco Bonadonna

### ► To cite this version:

Matthieu Berges, Rémi Choquet, Francesco Bonadonna. Impact of long-term behavioural studies in the wild: the blue petrel, *Halobaena caerulea*, case at Kerguelen. *Animal Behaviour*, 2019, 151, pp.53-65. 10.1016/j.anbehav.2019.03.004 . hal-02285159

**HAL Id: hal-02285159**

**<https://hal.science/hal-02285159v1>**

Submitted on 22 Oct 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

3

4 Matthieu Bergès, Rémi Choquet, Francesco Bonadonna\*

5

6 CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier -

7 EPHE – 1919 route de Mende, 34293 Montpellier cedex 5, France

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

19 \* Corresponding author: [Francesco.bonadonna@cefe.cnrs.fr](mailto:Francesco.bonadonna@cefe.cnrs.fr)

20

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,  $\Phi$ , the breeding probability conditional on  
195 survival,  $\Psi$ , 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  $\Phi$  (*transience x time x severity*),  
238  $\Psi$  (*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 ( $\Psi$ ) was determined starting from the model retained in the step. Fourth, the best  
243 effect for survival probability ( $\Phi$ ) 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,  $\Phi$ , the breeding probability conditional on survival,  $\Psi$ , 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  $\Phi$  (*transience x time x cumulative*),  $\Psi$  (*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 ( $\Psi$ ) was  
282 determined starting from the model retained in the step. Fourth, the best effect for survival  
283 probability ( $\Phi$ ) 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 ( $p\text{-value} = 0.051$ ). 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

#### 407 *Acknowledgements*

408 This work was financed by the French Polar Institute (IPEV): project ETHOTAAF  
409 354 to FB. We want to thank all the volunteers, students, and colleagues that worked with us  
410 on different subjects since 2006. We thank the Institut Polaire Français Paul-Emile VICTOR  
411 (IPEV) for logistic support. We also thank Nigel Gilles Yoccoz and two anonymous  
412 reviewers for improving the manuscript with their suggestions.

413

414

#### 415 **Bibliography**

416 Ackerman, J. T., Adams, J., Takekawa, J. Y., Carter, H. R., Whitworth, D. L., Newman, S.

417 H., . . . Orthmeyer, D. L. (2004). Effects of radiotransmitters on the reproductive

418 performance of Cassin's auklets. *Wildlife Society Bulletin*, 32(4), 1229-1241. doi: Doi

419 10.2193/0091-7648(2004)032[1229:Eorotr]2.0.Co;2

420 Adams, J., Scott, D., McKechnie, S., Blackwell, G., Shaffer, S. A., & Moller, H. (2009).  
421 Effects of geolocation archival tags on reproduction and adult body mass of sooty  
422 shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology*, 36(3), 355-366. doi:  
423 Doi 10.1080/03014220909510160

424 Akaike, H. (1987). Factor analysis and AIC. *Psychometrika* 52, 317–332.

425 Baker, G. B., Lumsden, L. F., Dettmann, E. B., Schedvin, N. K., Schulz, M., Watkins, D., &  
426 Jansen, L. (2001). The effect of forearm bands on insectivorous bats (Microchiroptera)  
427 in Australia. *Wildlife Research*, 28(3), 229-237. doi: Doi 10.1071/Wr99068

428 Barbraud, C., Rivalan, P., Inchausti, P., Nevoux, M., Rolland, V., & Weimerskirch, H.  
429 (2011). Contrasted demographic responses facing future climate change in Southern  
430 Ocean seabirds. *Journal of Animal Ecology*, 80(1), 89-100. doi: 10.1111/j.1365-  
431 2656.2010.01752.x

432 Barbraud, C., & Weimerskirch, H. (2003). Climate and density shape population dynamics of  
433 a marine top predator. *Proceedings of the Royal Society B-Biological Sciences*,  
434 270(1529), 2111-2116. doi: 10.1098/rspb.2003.2488

435 Barbraud, C., & Weimerskirch, H. (2005). Environmental conditions and breeding experience  
436 affect costs of reproduction in blue petrels. *Ecology*, 86(3), 682-692. doi: Doi  
437 10.1890/04-0075

438 Barron, D. G., Brawn, J. D., & Weatherhead, P. J. (2010). Meta-analysis of transmitter effects  
439 on avian behaviour and ecology. *Methods in Ecology and Evolution*, 1(2), 180-187.  
440 doi: 10.1111/j.2041-210X.2010.00013.x

441 Bonadonna, F., Caro, S., Jouventin, P., & Nevitt, G A. (2006). Evidence that blue petrel,  
442 *Halobaena Caerulea*, fledglings can detect and orient to dimethyl sulfide. *Journal of*  
443 *Experimental Biology*, 209, 2165-2169.

444 Bonadonna, F., & Mardon, J. (2010). One House Two Families: Petrel Squatters Get a Sniff  
445 of Low-Cost Breeding Opportunities. *Ethology*, 116(2), 176-182.

- 446 Bonadonna, F., Villafane, M, Bajzak, C, & Jouventin , P. (2004). Recognition of burrow's  
447 "olfactory signature" in blue petrels, *Halobaena caerulea*: an efficient discrimination  
448 mechanism in the dark. *Animal Behaviour*, *67*, 893-898.
- 449 Bried, J, & Jouventin , P. (2002). Site and mate-choice in seabirds: an evolutionary approach.  
450 In E. A. Schreiber & J. Burger (Eds.), *Biology of marine birds* (pp. 263-305). Boca:  
451 CRC Press.
- 452 Bried, J, Pontier, D, & Jouventin , P. (2003). Mate fidelity in monogamous birds: a re-  
453 examination of the Procellariiformes. *Animal Behaviour*, *65*, 235–246.
- 454 Brooke, M. (2004). *Albatrosses and Petrels across the World*. New York: Oxford University  
455 Press.
- 456 Burnham, K P , & Anderson, D R. (2002). *Model selection and Inference: A practical*  
457 *Information-theoretic approach. 2nd edition*. New York: Springer.
- 458 Cam, E., & Monnat, J. Y. (2000). Apparent inferiority of first-time breeders in the kittiwake:  
459 the role of heterogeneity among age classes. *Journal of Animal Ecology*, *69*(3), 380-  
460 394. doi: DOI 10.1046/j.1365-2656.2000.00400.x
- 461 Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Influence of body condition on  
462 reproductive decision and reproductive success in the Blue Petrel. *Auk*, *112*(4), 964-  
463 972.
- 464 Choquet, R, Rouan, L, & Pradel, R. (2009). Program E-SURGE: a software application for  
465 fitting multievent models. In D. L. Thomson, E. G. Cooch & M. J. Conroy (Eds.),  
466 *Modeling Demographic Processes in Marked Populations* (pp. 845–865). Berlin:  
467 Springer.
- 468 Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., & Pradel, R. (2009). U-CARE:  
469 Utilities for performing goodness of fit tests and manipulating CApture-REcapture  
470 data. *Ecography*, *32*(6), 1071-1074. doi: 10.1111/j.1600-0587.2009.05968.x



471 Converse, S. J., Kendall, W. L., Doherty, P. F., & Ryan, P. G. (2009). Multistate Models for  
472 Estimation of Survival and Reproduction in the Grey-Headed Albatross (*Thalassarche*  
473 *Chrysostoma*). *Auk*, *126*(1), 77-88. doi: 10.1525/auk.2009.07189

474 Croxall, J. P., Trathan, P. N., & Murphy, E. J. (2002). Environmental change and Antarctic  
475 seabird populations. *Science*, *297*(5586), 1510-1514. doi: DOI  
476 10.1126/science.1071987

477 Gabirot, M., Mardon, J., Campagna, S., West, N., Bonadonna, F., & Saunders, S M. (2016).  
478 Guidelines for collecting and extracting avian odors in remote field: Case study of a  
479 subantarctic seabird. In B. A. Schulte, T. E. Goodwin & M. H. Ferkin (Eds.),  
480 *Chemical Signals in Vertebrates XIII* (Vol. 13, pp. 435-460). Heidelberg: Springer.

481 Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013).  
482 Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues  
483 for homing after displacement. *Journal of Experimental Biology*, *216*(15), 2798-2805.  
484 doi: Doi 10.1242/Jeb.085738

485 Gauthier-Clerc, M., Gendner, J. P., Ribic, C. A., Fraser, W. R., Woehler, E. J., Descamps, S.,  
486 . . . Le Maho, Y. (2004). Long-term effects of flipper bands on penguins. *Proceedings*  
487 *of the Royal Society of London Series B-Biological Sciences*, *271*, S423-S426.

488 Green, J J, & Bradshaw, C J. (2004). The “capacity to reason” in conservation biology and  
489 policy: the southern elephant seal branding controversy. *Journal for Nature*  
490 *Conservation (Jena)*, *12*, 25-39.

491 Guinet, C., Chastel, O., Koudil, M., Durbec, J. P., & Jouventin, P. (1998). Effects of warm  
492 sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands.  
493 *Proceedings of the Royal Society B-Biological Sciences*, *265*(1400), 1001-1006. doi:  
494 DOI 10.1098/rspb.1998.0390

495 Jenouvrier, S., Barbraud, C., & Weimerskirch, H. (2005). Long-term contrasted responses to  
496 climate of two Antarctic seabird species. *Ecology*, *86*(11), 2889-2903. doi: Doi  
497 10.1890/05-0514

498 Kolliker, M., Brodie, E. D., & Moore, A. J. (2005). The coadaptation of parental supply and  
499 offspring demand. *American Naturalist*, 166(4), 506-516. doi: Doi 10.1086/491687

500 Le Bohec, C., Gauthier-Clerc, M., Gremillet, D., Pradel, R., Bechet, A., Gendner, J. P., & Le  
501 Maho, Y. (2007). Population dynamics in a long-lived seabird: I. Impact of breeding  
502 activity on survival and breeding probability in unbanded king penguins. *Journal of*  
503 *Animal Ecology*, 76(6), 1149-1160. doi: 10.1111/j.1365-2656.2007.01268.x

504 Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling Survival  
505 and Testing Biological Hypotheses Using Marked Animals - a Unified Approach with  
506 Case-Studies. *Ecological Monographs*, 62(1), 67-118. doi: Doi 10.2307/2937171

507 Leclaire, S., Bourret, V., & Bonadonna, F. (2017). Blue petrels recognize the odor of their egg.  
508 *Journal of Experimental Biology*, 220(17), 3022-3025. doi: 10.1242/jeb.163899

509 Leclaire, S., Strandh, M., Mardon, J., Westerdahl, H., & Bonadonna, F. (2017). Odour-based  
510 discrimination of MHC-similarity in birds. *Proceedings of the Royal Society B*, 284,  
511 2016-2466. doi: 10.1098/Rspb.2016.2466

512 Mardon, J., & Bonadonna, F. (2009). Atypical homing or self-odour avoidance? Blue petrels (  
513 *Halobaena caerulea*) are attracted to their mate's odour but avoid their own  
514 *Behavioral Ecology and Sociobiology*, 63, 537-542.

515 Mardon, J., Saunders, S M, & Bonadonna, F. (2011). From preen secretions to plumage: the  
516 chemical trajectory of petrels' social scent. *Journal of Avian Biology*, 42, 29-38.

517 Mardon, J., Saunders, S. M., Anderson, M. J., Couchoux, C., & Bonadonna, F. (2010).  
518 Species, Gender, and Identity: Cracking Petrels' Sociochemical Code. *Chemical*  
519 *Senses*, 35(4), 309-321.

520 Parris, K. M., McCall, S. C., McCarthy, M. A., Minter, B. A., Steele, K., Bekessy, S., &  
521 Medvecky, F. (2010). Assessing ethical trade-offs in ecological field studies. *Journal*  
522 *of Applied Ecology*, 47(1), 227-234. doi: 10.1111/j.1365-2664.2009.01755.x

523 Perry, G., Wallace, M. C., Perry, D., Curzer, H., & Muhlberger, P. (2011). Toe Clipping of  
524 Amphibians and Reptiles: Science, Ethics, and the Law. *Journal of Herpetology*,  
525 45(4), 547-555.

526 Pradel, R, Gimenez, O, & Lebreton, J D. (2005). Principles and interest of GOF tests for  
527 multistate capture–recapture models. *Animal Biodiversity and Conservation*, 28, 189-  
528 204.

529 Pradel, R. (2005). Multievent: An extension of multistate capture-recapture models to  
530 uncertain states. *Biometrics*, 61(2), 442-447. doi: 10.1111/j.1541-0420.2005.00318.x

531 Pradel, R., Cooch, E., & Cooke, F. (1995). Transient animals in a resident population of snow  
532 geese: Local emigration or heterogeneity? *Journal of Applied Statistics*, 22(5-6), 695-  
533 710. doi: Doi 10.1080/02664769524559

534 Ropert-Coudert, Y, Bost, C. A., Handrich, Y, Bevan, R. M., Butler, P. J., Woakes, A. J., & Le  
535 Maho, Y. (2000). Impact of externally attached loggers on the diving behaviour of the  
536 king penguin. *Physiological and Biochemical Zoology*, 73(4), 438-445.

537 Ropert-Coudert, Y., Knott, N., Chiaradia, A., & Kato, A. (2007). How do different data  
538 logger sizes and attachment positions affect the diving behaviour of little penguins?  
539 *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 54(3-4), 415-423. doi:  
540 10.1016/j.dsr2.2006.11.018

541 Sanz-Aguilar, A., Tavecchia, G., Genovart, M., Igual, J. M., Oro, D., Rouan, L., & Pradel, R.  
542 (2011). Studying the reproductive skipping behavior in long-lived birds by adding nest  
543 inspection to individual-based data. *Ecological Applications*, 21(2), 555-564. doi: Doi  
544 10.1890/09-2339.1

545 Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence  
546 stress responses? Integrating permissive, suppressive, stimulatory, and preparative  
547 actions. *Endocrine Reviews*, 21(1), 55-89. doi: Doi 10.1210/Er.21.1.55

548 Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beane, D., . . .  
549 Le Maho, Y. (2011). Reliability of flipper-banded penguins as indicators of climate  
550 change. *Nature*, 469(7329), 203-206. doi: 10.1038/nature09630

551 Stien, J., & Ims, R. A. (2016). Absence from the nest due to human disturbance induces  
552 higher nest predation risk than natural recesses in Common Eiders *Somateria*  
553 *mollissima*. *Ibis*, 158(2), 249-260. doi: 10.1111/ibi.12338

554 Strandh, M., Westerdahl, H., Pontarp, M., Canbäck, B., Dubois, M. P., Miquel, C., . . .  
555 Bonadonna, F. (2012). MHC class II but not class I predicts mate choice for  
556 compatibility in the olfactory oriented blue petrel, *Halobaena caerulea*  
557 (Procelariiformes) - as revealed by massively parallel pyrosequencing. *Proceedings of*  
558 *the Royal Society B*, 279, 4457–4463. doi: 10.1098/rspb.2012.1562

559 Wallace, B. P., Sotherland, P. R., Tomillo, P. S., Reina, R. D., Spotila, J. R., & Paladino, F.  
560 V. (2007). Maternal investment in reproduction and its consequences in leatherback  
561 turtles. *Oecologia*, 152(1), 37-47. doi: 10.1007/s00442-006-0641-7

562 Weimerskirch, H., Le Corre, M., Jaquemet, S., & Marsac, F. (2005). Foraging strategy of a  
563 tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine*  
564 *Ecology Progress Series*, 288, 251-261. doi: Doi 10.3354/Meps288251

565 Weimerskirch, H., Shaffer, S. A., Mabile, G., Martin, J., Boutard, O., & Rouanet, J. L.  
566 (2002). Heart rate and energy expenditure of incubating wandering albatrosses: basal  
567 levels, natural variation, and the effects of human disturbance. *Journal of*  
568 *Experimental Biology*, 205(4), 475-483.

569 Wilson, R. P., & McMahon, C. R. (2006). Measuring devices on wild animals: what  
570 constitutes acceptable practice? *Frontiers in Ecology and the Environment*, 4(3), 147-  
571 154. doi: Doi 10.1890/1540-9295(2006)004[0147:Mdowaw]2.0.Co;2

572

573

574

**Table1:** Description of the different severity classes

575

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

576

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).

583

584

585 **Appendix tables**

586  
587  
588  
589

**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	$\chi^2$	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

590  
591  
592  
593  
594  
595  
596

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.

597  
598  
599

**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:	<b>time x severity</b>	<b>188</b>	<b>4205.52</b>	<b>4656.64</b>	<b>1</b>	
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	
	<b>manipulated x time</b>	<b>183</b>	<b>4213.97</b>	<b>4650.79</b>	<b>12</b>	
	time x severity	183	4213.97	4650.79	13	
Step 3:	time x severity	183	4213.97	4650.79	13	
Breeding, $\Psi$	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	
	<b>time x breeder</b>	<b>169</b>	<b>4236.87</b>	<b>4634.42</b>	<b>20</b>	
	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, $\Phi$	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	
<b>three classes of manipulations + transience</b>		<b>109</b>	<b>4315.96</b>	<b>4557.36</b>	<b>33</b>	
three classes of manipulations x transience		113	4311.56	4562.80	34	
three classes of manipulations + transience <sup>(14)</sup>		98	4359.31	4574.04	35	
three classes of manipulations + transience <sup>(14)</sup>		101	4355.53	4577.48	36	
manipulated x transience <sup>(14)</sup>		97	4370.46	4582.80	37	
breeder x transience <sup>(14)</sup>		95	4372.53	4580.08	38	
manipulated x transience <sup>(14)</sup>	103	4350.60	4577.37	39		

600  
601  
602  
603  
604  
605  
606  
607  
608

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 ( $\Psi$ ) and Survival ( $\Phi$ ). The best structure for *p* were determined with the best structure for *e*, a time and a severity effect on  $\Psi$  and  $\Phi$ . The best structure for  $\Psi$  were determined with the best structure for *e* and *p* and a time and a severity effect on  $\Phi$ . The best structure for  $\Phi$  were determined with the best structure for *e*, *p* and  $\Psi$ . 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)).

610

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
	<b>time + cumulative</b>	<b>146</b>	<b>3815.98</b>	<b>4148.79</b>	<b>5</b>
	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
	<b>manipulated x time</b>	<b>138</b>	<b>3825.20</b>	<b>4139.72</b>	<b>14</b>
	Step 3:	time x cumulative	138	3825.20	4139.72
Breeding, $\Psi$	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
	<b>time x breeder</b>	<b>121</b>	<b>3847.79</b>	<b>4118.93</b>	<b>21</b>
	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, $\Phi$	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
	<b>breeder x transience</b>	<b>68</b>	<b>3900.72</b>	<b>4045.52</b>	<b>29</b>
	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	

611

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 ( $\Psi$ ) and Survival ( $\Phi$ ). The best structure for *p* were determined with the best structure for  
616 *m*, a time and a cumulative effect on  $\Psi$  and  $\Phi$ . The best structure for  $\Psi$  were determined with the best structure  
617 for *m* and *p* and a time and a cumulative effect on  $\Phi$ . The best structure for  $\Phi$  were determined with the best  
618 structure for *m*, *p* and  $\Psi$ .

619

620

621



622 **Figure legends**

623

624

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,  $\Phi$ , breeding probability,  $\Psi$ , 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.

630

631

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,  $\Phi$ , breeding probability,  $\Psi$ ,  
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.

637

638

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,  $\Delta$  for first class manipulate  
642 breeders,  $\nabla$  for second and third class manipulate breeders,  $\times$  for fourth class manipulate breeders. Solid lines  
643 represent the upper and lower confidence intervals (95%).

644

645

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.  $\Delta$  for non-manipulate breeder,  $\nabla$  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%).

651

652 **Appendix figure legends**

653

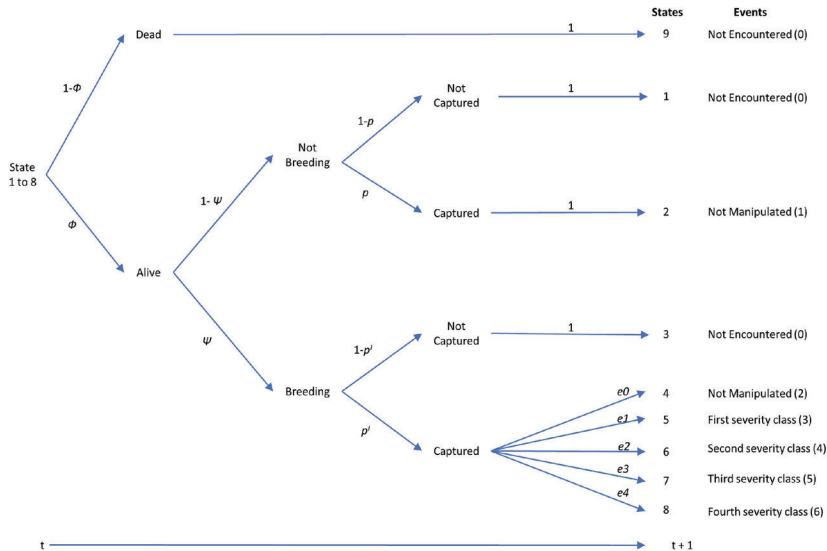
654 Figure A1: Model 1 implemented in E-SURGE; the model is a multi-event model. The  
655 matrices are Markovian and are used to study the potential effect of the different severity  
656 classes of manipulations on the blue petrel colony. Transition probabilities are separated in  
657 four matrices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

658

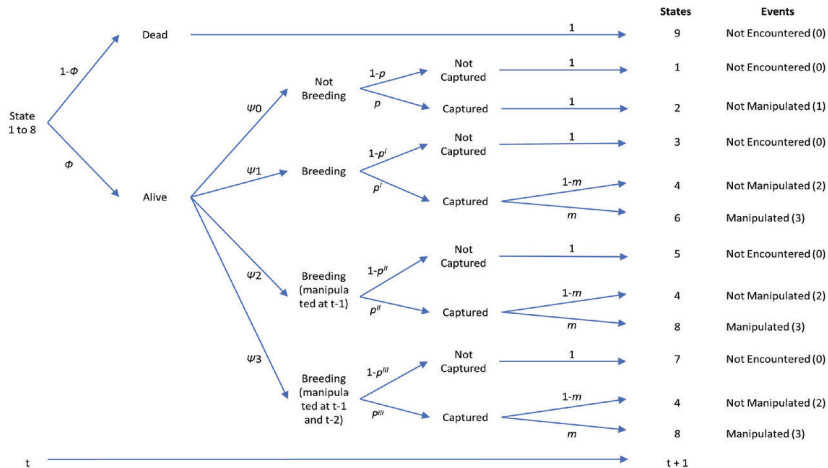
659

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



