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4 February 5, 2007

5 **Abstract**

6 In monomorphic species, determination of sex from behavior is prone to errors.  
7 Ignoring this fact renders problematic the estimation of sex-specific parameters.  
8 We develop capture-recapture survival models that account for uncertainty in the  
9 assessment of sex. There is a legitimate concern that some parameters may not  
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11 models with survival and encounter probabilities constant or time-dependent. We  
12 further develop a more refined and more appropriate model for an Audouin's gull  
13 data set where four distinct behavioral clues have been used. We examine how useful  
14 it is to incorporate the least reliable of the clues and the genetic determination of  
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# 18 **1 Introduction**

19 Sex differences in survival, dispersal or movement may have important consequences in  
20 demography, mating and parental investment patterns (Breitwisch, 1989; Gowaty, 1993),  
21 even for species where the two sexes have very similar body size and appearance. Thus,  
22 a modern study in ecology cannot ignore a priori this factor. However, naming the sex  
23 of an individual may be particularly tricky for monomorphic species observed in the  
24 field. Often the field biologist will rely on behavior to distinguish males from females.  
25 Some behavioral clues like position during copulation are thought to be quite reliable  
26 but other clues like the relative body size in a pair not so much and yet the latter type  
27 are easier to gather. With this kind of approach, it is thus not rare that an animal  
28 which has once been recorded as a male is later referred to as a female. Confidence in  
29 the correct determination of sex will progressively increase with repeated and consistent  
30 observations and, eventually, it may be decided that there is no reasonable doubt about  
31 the true sex of a particular individual. However, this does not hold for animals seen only  
32 a few times and for those with a contradictory record of given sex. A natural tendency for  
33 studying nonetheless sex-specific parameters is then to consider the sole individuals for  
34 which the sex has been determined with reasonable certainty. However, this approach has  
35 shortcomings, especially when the aim of the study is survival. First, it may represent  
36 a huge waste of data. For instance, in the field study that has motivated this paper,  
37 approximately 80% of the individuals had never been sexed and would thus be discarded.  
38 Second, to be sexed with reasonable certainty an individual must often have gone through  
39 several observations and hence have survived meanwhile. Then, estimation of survival  
40 based on the subsample of known-sex individuals will inevitably be biased high. Another  
41 possibility is to segregate the animals into three groups: males, females and unknown-  
42 sex individuals. The survival of the unknown-sex individuals can then be constrained  
43 to be a weighted average of the survivals of males and females (Oro and Pradel, 2000)  
44 with the weights reflecting the proportions of males and females among the unknown.  
45 However, these weights are not easy to determine as the relative proportions will depend  
46 on the sex-ratio but also on the relative catchability of males and females and on the

47 ability to identify the sex, which may differ between males and females. Thus, while this  
48 second method is preferable, it is still imperfect and anyway does not make full use of  
49 the information available.

50 We know of one example where sex uncertainty was directly incorporated in a survival  
51 analysis (Conroy et al., 1999). This study dealt with serins *Serinus serinus*, a species  
52 which is monomorphic only at the juvenile stage. A biometrical measure (wing length)  
53 was used to predict the sex of the captured juveniles and an initial state 'predicted male'  
54 or 'predicted female' was then assigned to each bird on this basis. If they were ever seen  
55 again, their true sex was then determined and they were assigned the new state 'known  
56 male' or 'known female'. This procedure allowed the estimation of transition probabilities  
57 between the 'predicted sexes' and the 'known sexes' and thus the incorporation of the  
58 never recaptured juveniles in the analysis. In this way, survival could be estimated without  
59 bias. This model was cast within the framework of multistate capture-recapture models  
60 (Arnason, 1972, 1973; Schwarz et al., 1993). Unfortunately, this approach does not work  
61 for species which remain monomorphic all their life and this is why we had to develop  
62 specific models. We present here a general solution to the problem of sex uncertainty  
63 by introducing explicitly probabilities of errors. In essence, as compared to previous  
64 approaches, instead of summarizing the data previous to the analysis, we model the very  
65 process of sex identification.

66 This work was motivated by the demographic study of an Audouin's gull *Larus au-*  
67 *douinii* colony at the Ebro Delta (Spain) (e.g. Oro and Pradel, 2000; Cam et al., 2004)  
68 where the birds are sexed upon observation according to four criteria (see Oro et al.,  
69 1999, for details): position during copulation, begging food during courtship, courtship  
70 feeding and relative body size (the males being on average slightly heavier than the fe-  
71 males, see Oro, 1998; Genovart et al., 2003a); or not sexed at all. The information can  
72 be coded as three basic events: "the animal is judged to be a male", "the animal is  
73 judged to be a female", "no judgment is issued". As this scheme should be relevant to  
74 many studies, we start (section 2) by developing a set of four general models that extend  
75 the Cormack-Jolly-Seber capture-recapture model and constant-parameter versions of it

76 (Cormack, 1964; Jolly, 1965, 1982; Seber, 1965) to uncertainty in sex assignment. These  
77 models incorporate probabilities of judgement and probabilities of error and can be fur-  
78 ther developed if needed. They are described in subsection 2.1. Because of the additional  
79 parameters involved, there is a legitimate concern that not all parameters may be iden-  
80 tifiable. In subsection 2.2, we set off to study redundancy by the method of Catchpole,  
81 Morgan and Freeman (1997; 1998). The models of subsection 2.1 do not account for likely  
82 differences in probability of error with each of the four criteria used in the Audouin’s gull  
83 study, nor do they incorporate such peculiarity of this study as a trend over time in the  
84 attempt to identify the sex of the birds. In the next section 3, we construct a more refined  
85 and more specialized model, suited to our data. At the same time, we assess the effect  
86 of dealing or not dealing with different pieces of information: is it useful to gather the  
87 least reliable clue? Should genetic sexing be developed? The last section is a discussion  
88 of the interest of this kind of models and of the implications of our findings in terms of  
89 field work.

## 90 **2 Four basic models**

### 91 **2.1 Description**

92 The typical data are presented in Fig. 1. There, the true sex of every single individual is  
93 unknown. To write the probability of a given encounter history  $h$ , we start by conditioning  
94 on the first capture event—as is usual in capture-recapture (CR)—and then apply the  
95 law of total probabilities:

$$96 \quad P(h) = P(f)P(h|f) + P(m)P(h|m).$$

97 Thus,  $P(f)$  and  $P(m)$  are the sex proportions among the unmarked captured, and  $P(h|f)$   
98 and  $P(h|m)$  are the conditional probabilities of  $h$  for a female and a male respectively.  
99 We need the following parameters:

100 1. Traditional CR parameters

- 101 •  $\phi_m, \phi_f$  sex-specific survival rates

$h$	$\#\{h\}$
0000033000	41
0000112133	4
0001011000	2
0033000300	8
0330003313	4
0102220203	1
1001101100	1

Figure 1: Excerpt from the Audouin’s gull data coded according to three criteria: 1=judged male; 2=judged female; 3=no judgement made.  $\#\{h\}$  is the number of individuals having encounter history  $h$ . The data set has 4025 individuals spread among 917 encounter histories over 10 years of study.

- 102           •  $p_m, p_f$  sex-specific encounter rates
- 103    2. New parameters
- 104           •  $\mu$ , proportion of males in the population
- 105           •  $e_m, e_f$  sex-specific probabilities to judge the sex of an individual
- 106           •  $x_m, x_f$  sex-specific probabilities to issue the correct judgement.

It is now possible to write out  $P(m)$  as  $\frac{p_m\mu}{p_m\mu+p_f(1-\mu)}$  ( $P(f) = 1 - P(m)$ ). As for the conditional probabilities, let us write them for  $h = 1\ 3\ 2$ . If this relates to a male, it has been sexed the first time (probability  $e_m$ ) correctly (probability  $x_m$ ). It has then survived to occasion 2 (probability  $\phi_m$ ), when it was encountered (probability  $p_m$ ), but not sexed (probability  $1 - e_m$ ). It survived again ( $\phi_m$ ), was encountered at occasion 3 ( $p_m$ ), and sexed ( $e_m$ ) incorrectly ( $1 - x_m$ ). All put together, we obtain  $P(h|m) = e_mx_m\phi_m p_m(1 - e_m)\phi_m p_m e_m(1 - x_m)$ . In a similar way, we would get  $P(h|f) = e_f(1 -$

$x_f)\phi_f p_f(1 - e_f)\phi_f p_f e_f x_f$ . The complete probability for this encounter history is thus

$$\begin{aligned}
 P(h) = & \frac{p_m \mu}{p_m \mu + p_f(1 - \mu)} e_m x_m \phi_m p_m (1 - e_m) \phi_m p_m e_m (1 - x_m) \\
 & + \frac{p_f(1 - \mu)}{p_m \mu + p_f(1 - \mu)} e_f(1 - x_f) \phi_f p_f(1 - e_f) \phi_f p_f e_f x_f.
 \end{aligned} \tag{1}$$

107 The probability of each individual encounter history will be obtained in this way and  
 108 hence the likelihood of the entire data set which, assuming independence of fates, is the  
 109 product of them. With  $\#h$  denoting the number of animals with encounter history  $h$ , the  
 110 likelihood can be written in compact form:

$$111 \quad L = \prod_h P(h)^{\#h}.$$

112 Maximum Likelihood Estimators (MLE) are derived by maximizing  $L$  as a function of the  
 113 different parameters. These estimators are known to have excellent statistical properties  
 114 such as being asymptotically unbiased and this is the approach to parameter estimation  
 115 retained in leading CR software. However, because the current models do not fall in the  
 116 category of existing models, we could not take advantage of this feature and wrote our  
 117 own maximizing programs in MATLAB (Hanselman and Littlefield, 2000).

## 118 **2.2 Parameter redundancy**

119 The aim of this subsection is to study the impact of the introduction of sex uncertainty  
 120 on parameter identifiability. As one can easily realize by browsing through the exten-  
 121 sive capture-recapture literature, the number of traditional CR models in use is virtually  
 122 unlimited as new models can be created by changing the kind of effects considered on  
 123 each type of parameters. For instance, parameters may be constant over time or time-  
 124 dependent; they may vary by sex, age... It is thus impossible to tell in advance which  
 125 parameters are or are not identifiable in each possible model. However, it is useful to have  
 126 some general guidance as to where problems are likely to occur. In traditional CR, the  
 127 fully time-dependent Cormack-Jolly-Seber model (CJS) plays this role. In this model, it  
 128 is known that survival over the last time interval is confounded with encounter probabil-  
 129 ity at the last occasion and it is a general feature of the fully time-dependent CR models



130 that the last interval is critical. This problem disappears if survival or encounter para-  
131 meters are hold constant. The introduction of sex uncertainty may well add new general  
132 identifiability problems. The minimal generalization of the CJS model consists in having  
133 the survival and encounter parameters, the 'traditional' parameters of subsection 2.1,  
134 still time-dependent and in considering that all of the 'new' parameters are constant over  
135 time. In this subsection, we examine whether this model is parameter-redundant. We  
136 also examine the three models derived by holding survival or encounter probabilities or  
137 both constant over time. In the following, we denote the four models considered by their  
138 sole variable part, i.e.  $(\phi_{t*s}, p_{t*s})$ ,  $(\phi_{t*s}, p_s)$ ,  $(\phi_s, p_{t*s})$ ,  $(\phi_s, p_s)$  where  $s$  stands for sex and  
139  $t$  for time.

140 Catchpole, Morgan and Freeman (1997; 1998) have developed a formal method (here-  
141 after the CMF method) for studying parameter redundancy in models belonging to the ex-  
142 ponential family of probability distributions. This method can be applied to the multino-  
143 mial distribution of animals over the observable encounter histories. It indicates which  
144 parameters are directly identifiable and provides identifiable functions of the redundant  
145 parameters (see Catchpole and Morgan (1997) and Catchpole et al. (1998) for details).  
146 All the calculations being formal, we carried them out with MAPLE. Because the number  
147 of capture histories  $4^k - 1$  increases rapidly with the number of time steps  $k$ , we could  
148 apply the procedure only for  $k = 3$ , but this is sufficient as the results obtained are easily  
149 demonstrated to hold in general.

150 A first conclusion (see Table 1) is that improving the realism of the models by adding  
151 new constant nuisance parameters to account for sex uncertainty does not restrict the  
152 ability to estimate the parameters of interest, i.e. the survival probabilities. Indeed, the  
153 only restriction we observe in the estimation of survival relates to the fully time-dependent  
154 model and this restriction is the same that was already present in the corresponding fully  
155 time-dependent CJS model. Actually, the new model improves over the CJS model ap-  
156 plied to each sex separately in allowing the estimation of the ratio of survivals of males  
157 and females at the last occasion; we believe that this result is due to the assumption of a  
158 constant sex-ratio in the population. The other case of parameter redundancy concerns

Table 1: Identification of estimable quantities in 4 models incorporating probabilities of error. Superscripts are for time steps. Only 3 occasions were considered.  $\phi^2$  and  $p^3$  are thus the last survival and last encounter parameters respectively.

Model	#par	Model rank	non estimable parameters	estimable functions
$(\phi_s, p_s)$	9	9	none	—
$(\phi_{t*s}, p_s)$	11	11	none	—
$(\phi_s, p_{t*s})$	13	12	$p_m^1, p_f^1$	$\frac{p_f^1}{p_m^1}$
$(\phi_{t*s}, p_{t*s})$	15	13	$p_m^1, p_m^3, p_f^1, p_f^3, \phi_m^2, \phi_f^2$	$\frac{p_f^1}{p_m^1}, \frac{\phi_f^2}{\phi_m^2}, \phi_m^2 p_m^3, \phi_f^2 p_f^3$

159 the initial encounter probabilities,  $p_m^1$  and  $p_f^1$  (absent from the CJS model). When en-  
160 counter probabilities are time-dependent (models  $(\phi_{t*s}, p_{t*s})$  and  $(\phi_s, p_{t*s})$ ), only the ratio  
161  $\frac{p_f^1}{p_m^1}$  i.e. the relative catchability of males and females at the initial occasion is estimable.  
162 This is easily understood from the likelihood. The initial encounter probabilities appear  
163 in it only in the terms  $P(m)$  and  $P(f)$ , and there only through their ratio. For instance,  
164  $P(m)$  can be rewritten

$$165 \quad P(m) = \frac{p_m \mu}{p_m \mu + p_f (1 - \mu)} = \frac{\mu}{\mu + \frac{p_f}{p_m} (1 - \mu)}.$$

166

### 167 2.3 Dual solutions

168 A redundant parameter is also one that can take all of a continuous range of values  
169 while the likelihood remains at its maximum. For a given data set, this can be seen  
170 by drawing the profile likelihood curve, i.e. the curve of the maximum value that the  
171 likelihood can assume for each value of the parameter under scrutiny: for a redundant  
172 parameter, the profile likelihood presents a characteristically flat area at its top. The  
173 shape of the profile likelihood is interesting more generally. For instance, when the profile  
174 likelihood decreases rapidly away from the optimal value of the parameter, this parameter  
175 is estimable with great precision. Away from its maximum, the profile likelihood may

176 exhibit local maxima. If one of these happens to be exactly on the same level as the  
177 'absolute' maximum, then this is an instance of non-identifiability without redundancy:  
178 two entirely different values of the parameter maximize the likelihood equally well but  
179 not the values in-between. This situation cannot be detected by the CMF method. Thus,  
180 we examined the profile likelihood curves of the model with traditional parameters hold  
181 constant  $(\phi_s, p_s)$  applied to the Audouin's gull data already mentioned (Fig. 1). The  
182 parameters were maintained within range by logit transformations. Instead of drawing  
183 the profile likelihoods, we actually drew the profile deviances ( $D = -2 \log L$ ) and hence  
184 observed the minima rather than the maxima (Fig. 2).

185 A striking feature of model  $(\phi_s, p_s)$  is the existence for each scalar parameter of two  
186 distinct values where the deviance is minimized. These values organize into two sets which  
187 represent two alternative solutions. This result is in fact data-independent and holds as  
188 well for the three other models of this section:  $(\phi_{t*s}, p_{t*s})$ ,  $(\phi_{t*s}, p_s)$  and  $(\phi_s, p_{t*s})$  (see the  
189 appendix for a theoretical demonstration). The deep reason for this fundamental duality  
190 comes down to this: given that the true sex of any individual is never known, it is equally  
191 acceptable, from the model point of view, to consider that an animal estimated many  
192 times to be, say, a male is indeed a male and that most judgments were correct, or that  
193 it is a female and most judgments were wrong. Yet, one solution produces probabilities  
194 of error above 50%, which is probably not acceptable from the practitioner's point of  
195 view. More precisely, one solution is derived from the other by exchanging the survival,  
196 encounter and judgment probabilities of males and females, replacing  $x_m$  with  $1 - x_f$  and  
197  $x_f$  with  $1 - x_m$  and finally reversing the sex-ratio (see Appendix). As a consequence, the  
198 profile deviance curves of sex-specific parameters are the same for males and females. In  
199 the case of the Audouin's gull data, they present two close minima (Fig. 2). The profile  
200 deviance curve of the proportion of males is symmetrical around 0.5 with two minima,  
201 which happen to be very distant with our data, at 0.14 and 0.86, and, incidentally, utterly  
202 unrealistic from a biological point of view.

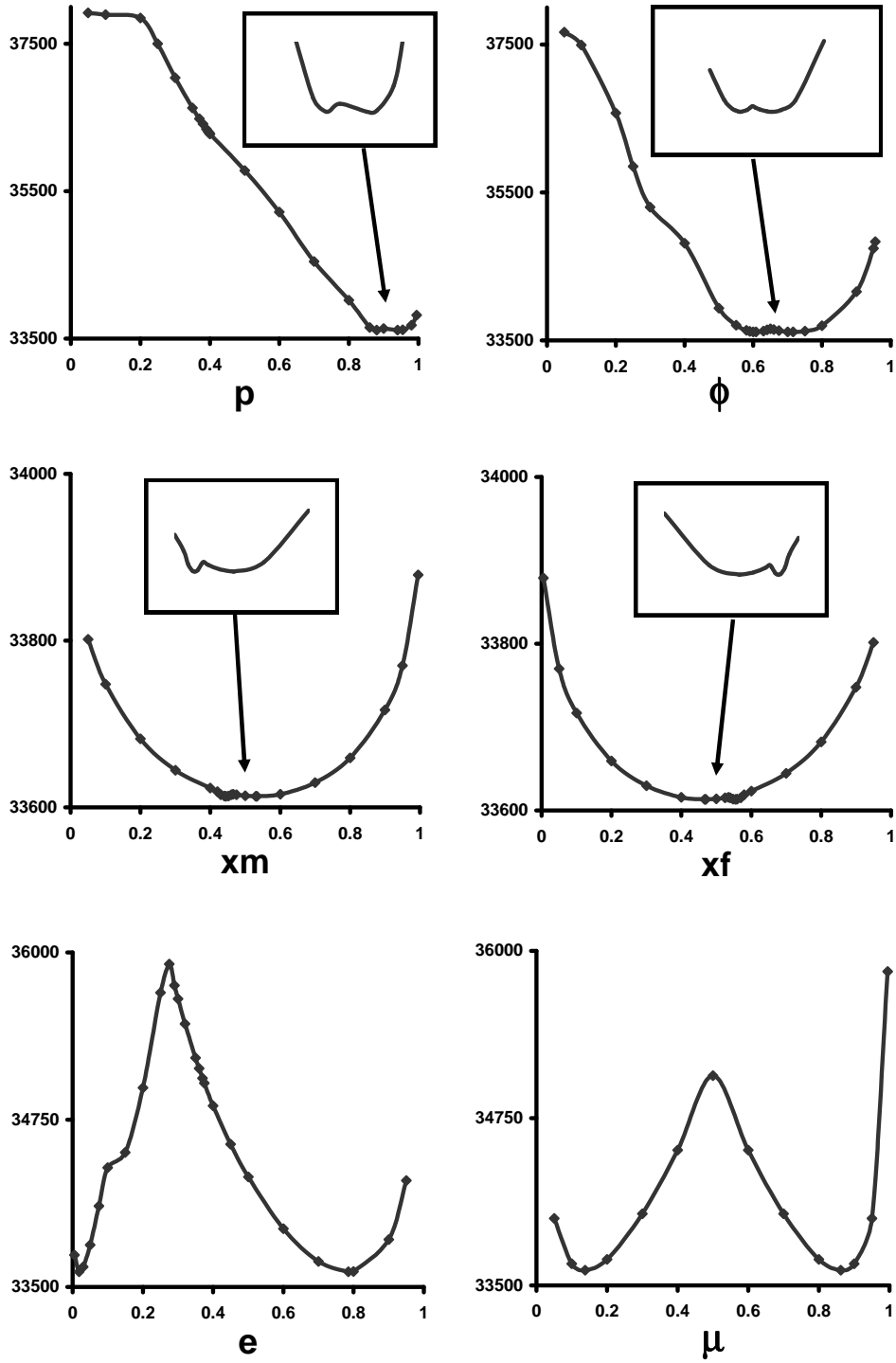


Figure 2: Profile-deviance curves of the parameters of model  $(\phi_s, p_s)$  applied to the Audouin's gull data set. For each parameter, the deviance (y-axis) presents two distinct minima. The curves for  $p$ ,  $\phi$  and  $e$  are the same for males and females.

Table 2: Maximum-likelihood estimates for each of the four models. For time-dependent parameters, the median is given. Each model has also a dual solution with probabilities of errors  $>50\%$ .

Model	encounter		survival		probability		probability		proportion
	probability		$(\phi)$		of judgment		to be right		of males
	(p)				(e)		(x)		$(\mu)$
	m	f	m	f	m	f	m	f	(m)
$(\phi_s, p_s)$	0.61	0.72	0.88	0.95	0.02	0.79	0.53	0.56	0.86
$(\phi_{t*s}, p_s)$	0.60	0.72	0.89	0.97	0.02	0.79	0.53	0.56	0.87
$(\phi_s, p_{t*s})$	0.61	0.74	0.87	0.95	0.02	0.79	0.53	0.56	0.88
$(\phi_{t*s}, p_{t*s})$	0.61	0.76	0.86	0.97	0.02	0.79	0.53	0.56	0.88

### 203 3 A more realistic model for the Audouin’s gull data

204 The four models introduced in the previous section, fitted to the Audouin’s gull data,  
205 produce very unreasonable if similar estimates: very high proportions of males that are  
206 almost never judged and probabilities of error close to 50% (Table 2). This is not entirely  
207 surprising given that they do not incorporate several known important features of the  
208 study. In this section, we exemplify the flexibility of our approach by building a more  
209 realistic model incorporating our knowledge of the biology and of the way the field work  
210 had been conducted.

211 To start, there was no good reason to believe that the error attached to each of the  
212 4 criteria used (copulation, begging food, courtship feeding and relative body size) was  
213 the same. Copulation for instance was suspected to be the most reliable and relative  
214 body size, the most error-prone. We thus decided to distinguish the different criteria and  
215 recoded the data accordingly (see Table 3). All along the study, sex determination has  
216 been a secondary activity but it has been conducted on stringent criteria. This is reflected  
217 in the very few obvious mistakes (sexing is consistent over time for a given individual),  
218 but the roughly 80% of never-sexed individuals in the data set. Yet, during the course of

Table 3: Codes used to take into account the unequal reliability of each of the 4 criteria used to assess the sex of Audouin’s gulls upon observation at the Ebro delta colony (Spain).

judged from	to be		not judged
	m	f	
copulation	1	5	9
begging food	2	6	
courtship feeding	3	7	
body size	4	8	

219 the study, sexing has gained ground; especially the criterion ‘relative body size’, initially  
 220 used very sparingly, has become more common by the end of the study. These features  
 221 were incorporated in a model denoted  $(\phi_s, p_t, \mu, e_T, m4_T, m1, m2, x1, x2, x3, x4)$  with  
 222 the following characteristics:

- 223 •  $p_t$ , encounter probability: time but not sex-dependent.
- 224 •  $\phi_s$ , survival rate: possibly sex-dependent but constant over time.
- 225 •  $\mu$ , proportion of males: held constant.
- 226 •  $e_T$ : logit-linear trend over time ( $T$ ) in the attempt to judge the sex ( $e$ ). Note that  
 227 because birds are always judged by pair, we put no sex-dependency on  $e$ .
- 228 •  $m4_T$ : logit-linear trend over time ( $T$ ) in the frequency of use of the criterion ‘relative  
 229 body size’ ( $m4$ ) among the instances when a judgment was issued.
- 230 •  $m1$ : frequency of use of the criterion ‘copulation’ among the behavioural criteria  
 231 (i.e. excluding ‘body size’): held constant.
- 232 •  $m2$  and  $m3$ : same as  $m1$  for ‘begging food’ and ‘courtship feeding’ respectively (one  
 233 of  $m1, m2$  or  $m3$  is redundant).
- 234 •  $x_i$ : probability to be right when using criterion  $i$  ( $i = 1, \dots, 4$ ): held constant.

235 This model has 23 parameters including 1 intercept and 1 slope for  $e$  and 1 intercept and  
236 1 slope for  $m_4$  and 10 capture probabilities.

237 Additionally, a very few birds (24) had been sexed genetically (Genovart et al.,  
238 2003*a,b*). We fitted the previous model using (analysis A) and not using (analysis B)  
239 this limited information. When we used it,  $P(m)$  in the capture history of the genetically  
240 sexed individuals was set to 1 or 0 as appropriate. On the other hand, we considered the  
241 effects of not using the presumably less reliable criterion, 'body size'. To do that, the  
242 corresponding observations were recoded as a 'no judgment' observation. When doing  
243 this latter analysis (analysis C), the genetic determination of sex was not used. Thus,  
244 we have a gradient of decreasing amount of information from analysis A to analysis C  
245 (Table 4).

246 All three analyses yield estimates in agreement with what is known of the biology of  
247 the species. For instance, survival estimates are very close to those estimated previously  
248 by CR in the study site (e.g. Oro et al., 1999; Cam et al., 2004). We also note that,  
249 as anticipated, body size is the least reliable clue but the copulation criterion does not  
250 come out as the obvious best method. The results with and without genetical information  
251 are very similar (first 2 columns of Table 4). However, the known sex of only 24 birds  
252 suffices to break the tie between the dual solutions: while analyses B and C still have  
253 two solutions (only the reasonable one is presented in Table 4), analysis A has just one,  
254 as can be seen on the profile deviance curves relative to the proportion of males (Fig. 3).  
255 In other, not shown models, where sex-ratio is initially not identifiable, the additional  
256 information brought about by the 24 birds renders this and other parameters identifiable.  
257 As for the criterion 'body size', even though mistakes are made on average once in every  
258 10 judgments and only 15.70% of the judgments made use this criterion, dropping it  
259 results in a disproportionate loss of precision (compare the standard errors in the last two  
260 columns of Table 4).

Table 4: Results of model  $(\phi_s, p_t, \mu, e_T, m_{4T}, m_1, m_2, x_1, x_2, x_3, x_4)$  applied to the Audouin’s gull data set with different amount of information. Analysis A uses all 4 criteria and the genetic determination of the sex of 24 birds; Analyses B and C do not use the genetic determination of sex; Analysis C does not use the judgments based on body size. Standard errors are given between parentheses. With less information (from left to right), precision decreases. For analyses B and C, we have retained the dual solution that yields proportions of error  $<50\%$ .

Analysis	A	B	C
proportion of males	0.53 (0.027)	0.53 (0.029)	0.55 (0.034)
female survival	0.91 (0.013)	0.91 (0.014)	0.93 (0.024)
male survival	0.86 (0.013)	0.86 (0.014)	0.84 (0.025)
error copulation	0.06 (0.041)	0.06 (0.041)	0.08 (0.055)
error begging food	0.05 (0.029)	0.06 (0.031)	0.09 (0.077)
error courtship feeding	0.00 (0.161)	0.00 (0.155)	0.00 (0.286)
error body size	0.11 (0.064)	0.09 (0.074)	NA



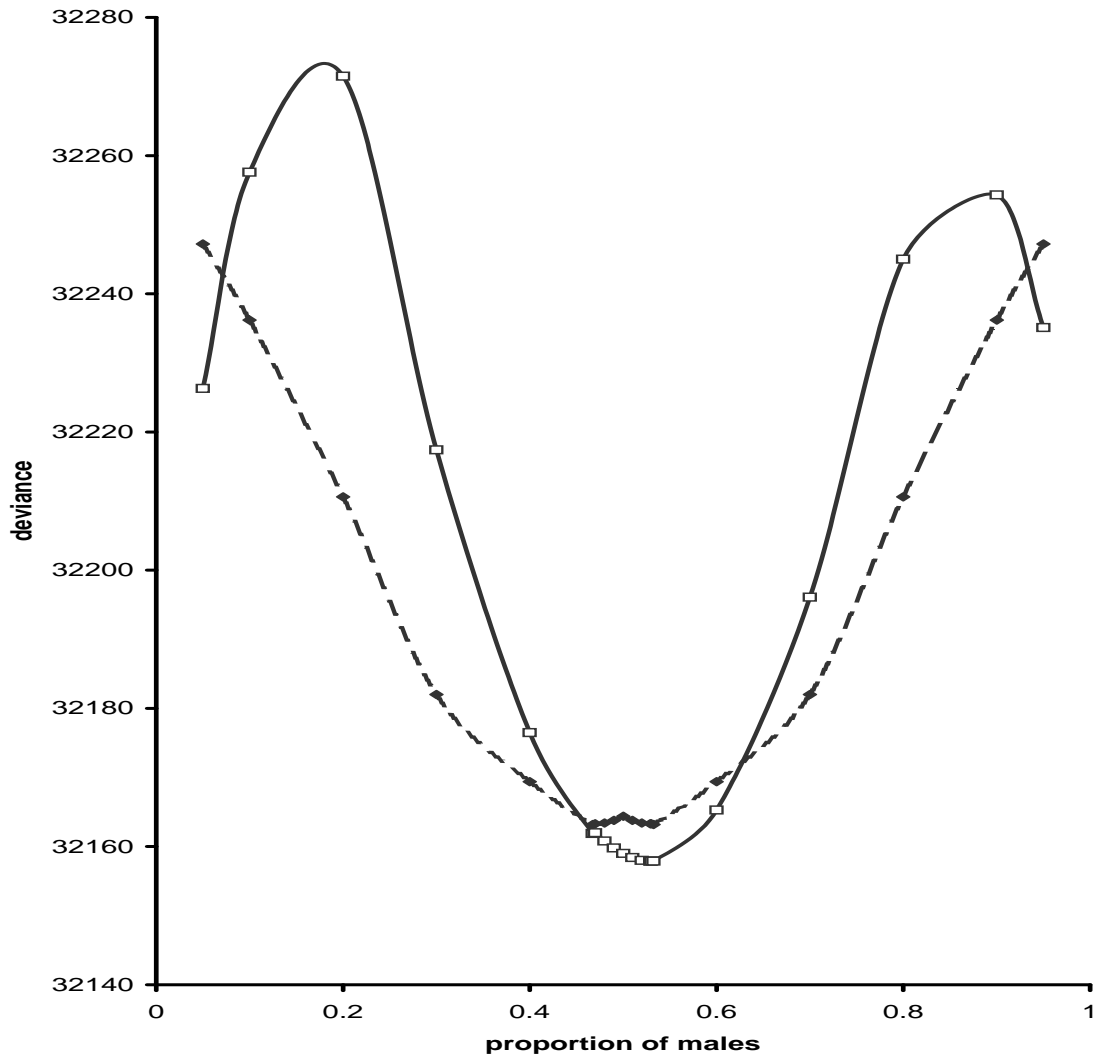


Figure 3: Improvement in the shape of the deviance brought about by a limited amount of external information shown on the profile deviance of model  $(\phi_s, p_t, \mu, e_T, m4_T, m1, m2, x1, x2, x3, x4)$  applied to the Audouin's gull data set and relative to the proportion of males  $\mu$ . The genetic sexing of 24 individuals renders the profile deviance steeper at its bottom where it retains just one minimum (Analysis A; continuous line) as compared to when the genetic information is not used (Analysis B; dotted line). There is a narrow ridge between the 2 dual solutions in Analysis B.

## 261 4 Discussion

262 A main concern when we started building these models was the risk of parameter redun-  
263 dancy. The models would have been useless if no parameter of interest was estimable.  
264 This fear had been voiced in particular by Nichols et al. (2004) when they examined  
265 the restricted situation where the sex is not always assessed but, if so, without error.  
266 Our results show on the contrary that it is quite possible to run models incorporating  
267 probabilities of error and nonetheless gain knowledge about such important biological  
268 parameters as survival rates. Although these models have in general two mathematical  
269 solutions, one is so unreasonable that it should not be difficult to sort out which one is  
270 to be retained.

271 A more serious difficulty is numerical. These models, and more generally the mul-  
272 tievent models (Pradel, 2005) to which they belong—but also the now classical multi-  
273 state models—present local minima to which the optimization algorithm occasionally  
274 converges. The profile deviance curves may help diagnose the problem and improved  
275 algorithms may be sought (see, in particular, section 6.2 in Choquet et al., 2005), but it  
276 is also possible to guard against local minima by augmenting the information available.  
277 Often, such information already exists, but could not be exploited in the traditional CR  
278 models. One of the major aims of the newly developed models was indeed to alleviate  
279 and valorize the field work by comprehending and exploiting a wider range of data.

280 In this paper, we have examined two ways of gathering additional information: us-  
281 ing less efficient clues and sexing genetically some animals. Genetic sexing is of course  
282 paramount for the determination of sex, but for practical reasons it cannot usually be  
283 performed on every single individual. In our example, genetically sexing very few birds  
284 proved sufficient to greatly improve the shape of the deviance and hence the efficiency of  
285 the optimization algorithm. We also observed that it eliminated the wrong one of the two  
286 dual solutions. Finally, genetic sexing occasionally rendered identifiable new parameters  
287 in parameter-redundant models. It should also be noticed that genetic sexing is only one  
288 approach to specifying the a priori probability to be a male,  $P(m)$ , for some individu-  
289 als. Other, not necessarily 0 – 1 predictors of sex frequently available in old studies, like

290 biometrical measures, can be incorporated in the model in the same way ( $P(m)$  can be  
291 set to some intermediate value between 0 and 1). This approach of incorporating exter-  
292 nal information has been used by Fujiwara and Caswell (2002) although in a way that,  
293 past the first encounter, may not be correct: the conditioning in their stage-assignment  
294 matrix,  $P(stage|measure)$ , is the reverse of what is needed,  $P(measure|stage)$ , in the  
295 calculation of the likelihood (see Pradel, 2005, for a formal demonstration). As for the  
296 use of less efficient clues, our example proved that they may be valuable beyond what  
297 seems at first sight attainable based on their frequency of use and efficiency (percentage  
298 of error). We thus encourage people to gather such clues especially if they are not time  
299 consuming (e.g. Redman et al., 2002). After three or four visits, it will always be possible  
300 to assess the quality of the prospective clues as well as the improvement brought about  
301 by such and such identification method in terms of gained precision. If different methods  
302 for sex identification are in competition, it is then possible to decide objectively, from the  
303 informed assessment of their relative costs and benefits, which ones to favor and which  
304 ones to discard.

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## 358 **Appendix**

359 The aim of this appendix is to establish the existence of two distinct dual solutions to  
 360 the maximization of the likelihood of model  $(\phi_s, p_s)$  presented in subsection 2.1, as well  
 361 as some related properties of its profile deviance curves. Why this happens is rooted in  
 362 the law of total probabilities applied to an arbitrary encounter history  $h$ .

363 
$$P(h) = P(f)P(h|f) + P(m)P(h|m)$$

364 In this formula, the conditional probability  $P(h|f)$  is a function of the sole parameters  
 365  $\phi_f, p_f, e_f, x_f$ . This function depends on the particular encounter history  $h$ . Let write

$$366 \quad P(h|f) = g_h(\phi_f, p_f, e_f, x_f). \quad (2)$$

367 The probability of the same history conditional on the animal being this time a male  
 368 is obtained by using the male parameters instead of the female ones. However, when a  
 369 judgment was right for a female, it is wrong for a male (and vice-versa) so that  $x_f$  should  
 370 be replaced with  $1 - x_m$  (see the example of section 2.1 leading to equation 1 if this is  
 371 not immediately clear). Thus,

$$372 \quad P(h|m) = g_h(\phi_m, p_m, e_m, 1 - x_m). \quad (3)$$

373 The unconditional probabilities  $P(m)$  and  $P(f)$  are respectively

$$374 \quad \frac{p_m \mu}{p_m \mu + p_f(1 - \mu)} \text{ and } \frac{p_f(1 - \mu)}{p_m \mu + p_f(1 - \mu)}. \quad (4)$$

375 The transformation  $\Theta: [0, 1]^9 \longrightarrow [0, 1]^9$

$$376 \quad (\theta_1, \dots, \theta_9) \mapsto (\theta_2, \theta_1, \theta_4, \theta_3, 1 - \theta_5, \theta_7, \theta_6, 1 - \theta_9, 1 - \theta_8)$$

377 plays a key role. We first establish

378 **Lemma 1.** *The probability of any encounter history, seen as a function of the parameter*  
 379 *vector  $(\phi_m, \phi_f, p_m, p_f, \mu, e_m, e_f, x_m, x_f)$ , is invariant under  $\Theta$ .*

$$380 \quad \forall h, P(h) \circ \Theta = P(h)$$

381 *Proof.* When the parameters are changed in the following way:

$$382 \quad (\phi_m, \phi_f, p_m, p_f, \mu, e_m, e_f, x_m, x_f) \xrightarrow{\Theta} (\phi_f, \phi_m, p_f, p_m, 1 - \mu, e_f, e_m, 1 - x_f, 1 - x_m),$$

$$384 \quad P(f) \text{ becomes } \frac{p_m \mu}{p_m \mu + p_f(1 - \mu)} = P(m); \quad [\text{from (4)}]$$

$$385 \quad P(m) \text{ becomes } \frac{p_f(1 - \mu)}{p_m \mu + p_f(1 - \mu)} = P(f); \quad [\text{from (4)}]$$

$$386 \quad P(h|f) \text{ becomes } g_h(\phi_m, p_m, e_m, 1 - x_m) = P(h|m); \quad [\text{from (2) and (3)}]$$

$$387 \quad P(h|m) \text{ becomes } g_h(\phi_f, p_f, e_f, x_f) = P(h|f); \quad [\text{from (2) and (3)}]$$

389 so that, eventually,  $P(h)$  itself is unchanged. □

390 A consequence of this lemma is that the likelihood and the deviance are equally un-  
391 changed under  $\Theta$ . Consequently, if the parameter vector  $(\hat{\phi}_m, \hat{\phi}_f, \hat{p}_m, \hat{p}_f, \hat{\mu}, \hat{e}_m, \hat{e}_f, \hat{x}_m, \hat{x}_f)$   
392 maximizes the likelihood, its transform by  $\Theta$ ,  $(\hat{\phi}_f, \hat{\phi}_m, \hat{p}_f, \hat{p}_m, 1 - \hat{\mu}, \hat{e}_f, \hat{e}_m, 1 - \hat{x}_f, 1 - \hat{x}_m)$ ,  
393 maximizes it too. Hence, the theorem:

394 **Theorem 1.** *The likelihood of model  $(\phi_s, p_s)$  is maximized at two generally distinct points*  
395 *one of which is the transform of the other by the unipotent mapping  $\Theta$ .*

396 We now examine some ensuing properties of the profile deviance curves. Let  $D$  be  
397 the deviance of model  $(\phi_s, p_s)$ .  $D: [0, 1]^9 \rightarrow [0, +\infty]$ , is a function of the 9 probability  
398 parameters:  $\phi_m, \phi_f, p_m, p_f, \mu, e_m, e_f, x_m, x_f$ , which has the property that  $D \circ \Theta = D$ . If

$$399 \quad E_i^a = \{\theta \in [0, 1]^9, \theta_i = a\},$$

400 the profile deviance function for parameter  $i$  is

$$401 \quad P_i(a) \stackrel{\text{def}}{=} \min_{E_i^a} D = \min_{E_i^a} (D \circ \Theta) = \min_{\Theta(E_i^a)} D.$$

402 Given that:

$$403 \quad \Theta(E_1^a) = E_2^a, \quad \Theta(E_2^a) = E_1^a,$$

$$404 \quad \Theta(E_3^a) = E_4^a, \quad \Theta(E_4^a) = E_3^a,$$

$$405 \quad \Theta(E_5^a) = E_5^{1-a},$$

$$406 \quad \Theta(E_6^a) = E_7^a, \quad \Theta(E_7^a) = E_6^a,$$

$$407 \quad \Theta(E_8^a) = E_9^{1-a}, \quad \Theta(E_9^a) = E_8^{1-a},$$

409 then,

$$410 \quad P_1(a) = \min_{E_2^a} D = P_2(a),$$

$$411 \quad P_3(a) = \min_{E_4^a} D = P_4(a),$$

$$412 \quad P_5(a) = \min_{E_5^{1-a}} D = P_5(1 - a),$$

$$413 \quad P_6(a) = \min_{E_7^a} D = P_7(a),$$

$$414 \quad P_8(a) = \min_{E_9^{1-a}} D = P_9(1 - a).$$

415

416 Thus, the profile deviances of the survival (parameters 1 and 2), encounter (parameters 3  
417 and 4) and judgment probabilities (parameters 6 and 7) are the same for both sexes. The  
418 profile deviance of the probability of error for the males (parameter 8) is the symmetrical  
419 with respect to  $a=0.5$  of that for the females (parameter 9), and the profile deviance  
420 curve of the proportion of males (parameter 5) is symmetrical with respect to  $a=0.5$ .