

1 **Better together: a transboundary approach to brown bear monitoring in the** 2 **Pyrenees**

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34 **Abstract**

35 Human administrative borders have no effect on wild animals, and the vast home ranges of large carnivores
36 often cause them to live simultaneously on the territory of two or more countries or jurisdictions with
37 different management policies. Here, we investigate the importance of transboundary population monitoring
38 using as a case study the Pyrenean brown bear population (*Ursus arctos*) that lives in France, Andorra and
39 Spain. Using capture-recapture models and the Pollock's robust design, we estimated abundance and
40 demographic parameters using data collected separately in France and Spain and a dataset gathered from
41 joint monitoring on both sides of the border. As expected, the abundance estimates from French (from 11
42 bears in 2008 to 13 in 2014) or Spanish (from 4 bears in 2008 to 9 in 2014) data only were lower than
43 abundance obtained from both sides of the border (from 11 in 2008 to 18 in 2014). The joint monitoring
44 dataset also highlighted the importance of individual detection heterogeneity that, if ignored, would lead to
45 underestimation. Our results reinforce the importance of transboundary cooperation when dealing with
46 animal populations with territory spanning two or more administrative jurisdictions for collecting reliable
47 scientific data and providing relevant abundance estimation to take sound management decisions.

48 *Keywords: capture-recapture, elusive species, robust design, transboundary monitoring, Ursus arctos*

49 **Introduction**

50 Large carnivore populations in Europe are recovering from years of decrease after having been highly
51 threatened or locally extinct, leading to larger population sizes and wider distributions (Chapron et al. 2014).
52 These populations have large home ranges despite interspecific (Gittleman and Harvey 1982) or intraspecific
53 (Mattisson et al. 2013; Nilsen et al. 2005) variations, and their recovery increases the likelihood of crossing
54 the administrative border between two countries, or between two distinct jurisdictions within the same
55 country. Therefore, the same large carnivore population may overlap several territories where the inhabitants
56 have different or conflicting opinions on their monitoring or management (Bischof and Swenson 2012; Bull
57 et al. 2009; Piédallu et al. 2016).

58 The conservation status of a population is commonly estimated based on its abundance and distribution,
59 which in turn may help to assess its viability and to predict its range in the future. However, while
60 transboundary large carnivore populations are extremely common, transboundary conservation policies are

61 still rarely implemented (Gervasi et al. 2015; Linnell and Boitani 2012; Trouwborst 2010). Moreover,
62 population monitoring is usually performed independently between the countries on one side and the other of
63 the boundary. These countries in turn perform abundance estimation based solely on the data gathered on
64 their own territory, leading to a discrepancy between management policy and ecological reality (Linnell and
65 Boitani 2012; Trouwborst 2010). This approach might cause significant errors when trying to assess the
66 abundance of a species, due to the possibility for a single animal to be seen across different territories
67 (Bischof et al. 2016).

68 Here, we aimed at illustrating the value of collaborative monitoring at a transboundary scale, using brown
69 bears (*Ursus arctos*) in the Pyrénées as a case study. Brown bears are widely distributed in the Northern
70 hemisphere, being spread over North America (Waits et al. 1998), Europe (Swenson et al. 2011), and Asia
71 (Hirata et al. 2013). The species as a whole is not endangered. However, some populations can be both small
72 and isolated from others, leading to an important risk of local extinction (Linnell et al. 2008; Swenson et al.
73 2011). Among those endangered populations is the Pyrenean brown bear population, which resides in the
74 mountains between Southwestern France and Northeastern Spain. Despite being reinforced by the
75 reintroduction of individuals from Slovenia in 1996-97 (3 bears) and 2006 (5 bears) with another one
76 scheduled for 2016 (1 bear), its viability is still considered to be low (Chapron et al. 2010) due to its small
77 size, its fragmentation in different cores, and heavy inbreeding that might negatively impact its growth in a
78 medium- or long-term future. Moreover, there are conflicting attitudes among local inhabitants over bear
79 presence (Piédallu et al. 2016).

80 Combining data collected through camera trapping, systematic search-effort protocols and opportunistic
81 observations in Spain and France, we estimated abundance and demographic parameters for the Pyrenean
82 brown bear population using Pollock's robust design capture-recapture models (Kendall et al. 1997). We
83 reproduced the same analyses mimicking a lack of collaboration between the two countries and compared the
84 results. Overall, we demonstrate the benefits of cooperation across the border in the monitoring and
85 management of a large carnivore population.

86 **Material & Methods**

87 1. Study area and bear population

88 This study was performed in the Pyrenees Mountains, on both sides of the border, which included
89 Southwestern France, the North of the Spanish Autonomous communities of Catalonia, Aragon and Navarre,
90 and the principality of Andorra (Figure 1). Bears that live in the Pyrenees descend from individuals that were
91 translocated here from Slovenia in 1996-97 (2 females and 1 male) and 2006 (4 females and 1 male),
92 although a hybrid between a Slovenian bear and a now-deceased Pyrenean female is still alive. The
93 relocations were performed to save the population that was in critical danger of extinction in 1995, with only
94 5 individuals remaining, including a single adult female. The current population is split in two unconnected
95 population cores(Camarra et al. 2015): one in the Western Pyrenees, over France, Aragon and Navarre, and
96 one in Central-Eastern Pyrenees, over France, Catalonia, Aragon and Andorra.

97 2. Data collection and monitoring

98 Systematic monitoring was performed in France, Catalonia and Andorra from 2008 to 2014, consisting in
99 fixed itineraries along which agents of governmental wildlife looked for bear tracks with help on the French
100 side of the Pyrenees from volunteers of the Brown Bear Network, whose members include 135 professional
101 members (from various agencies) and 228 amateur members (who are not affiliated to any agency). In
102 Catalonia, two teams of 10 professional members handle systematic monitoring with help from Forestry
103 Agents. Visits of these itineraries were repeated at regular time intervals between April and November, with
104 at least a monthly visit (Figure 1). Due to the very low number of bears on their territories, there was no
105 systematic monitoring in Aragon and Navarre. In all areas, data was also obtained through opportunistic
106 means, which included all sightings or tracks found outside of systematic monitoring and validated by the
107 local agencies, or damages caused on livestock (sheep in particular) or beehives. Since 2008, both countries
108 have worked to standardize their monitoring protocols in the framework decided by the Transborder
109 Monitoring Group for Bears in Pyrenees (GSTOP).

110 The most common bear tracks included hair samples (with 4-5 hair traps being scattered along the itineraries
111 to improve the chances of getting a sample), scats, footprints, claw marks, photographs, films, attacks on
112 livestock, sightings and opened ant-hills. Hair traps were added on trees along the itineraries to increase the
113 chances to obtain hair samples. We discarded the tracks that did not allow the identification of an individual,
114 mostly due to a lack of a good enough genetic sample. We also paid a particular attention to estimate the

115 interval in which the bear might have left the track (see Supplementary materials). Genetic samples (hairs
116 and faeces) were analyzed using a Polymerase Chain Reaction (PCR) multitube approach with four repeats
117 for each sample to avoid the risk of misidentification due to the low DNA quantity of some hair samples
118 (Miquel et al. 2006; Taberlet et al. 1997). 13 microsatellites markers and 1 marker for sex were targeted by
119 the PCR in order to identify the bear individuals. The results were then aggregated between all sources.

120 We assigned to each individual its age class at first capture (Cub: up to 1 year old, Juvenile: up to 3 years
121 old, Adult: 4 years old and more) and its gender. The population was assumed geographically closed, i.e. no
122 emigration or immigration between this population and another one outside the Pyrenees.

123 3. Abundance estimation

124 We used the Pollock's robust design (Kendall et al. 1997) to estimate abundance while accounting for
125 imperfect detection of individuals and temporary emigration. The robust design approach uses repeated
126 captures in a short timeframe, called secondary occasions, within a single time step (a so-called primary
127 occasion). The population is considered to be closed (without demographic processes such as births, deaths,
128 immigrations and emigrations) between two consecutive secondary occasions, hence allowing the robust
129 estimation of abundance corrected for imperfect detection, and open (with births, deaths, emigrations and
130 immigrations) between two consecutive primary occasions. In this study, we used years as primary occasions
131 of capture (7 in total, from 2008 to 2014) and the months from May to September as secondary occasions (5
132 in total). We chose these secondary occasions because no births occur in this time interval, and we did not
133 include the first months of the year because very young cubs have a high risk of dying.

134 We built three capture-recapture datasets: one for French data (including Andorra), one for Spanish data
135 (Catalonia, Aragon, Navarre), and one for the Combined (France and Spain) data. We tested three possible
136 types of temporary emigration: no emigration, a random emigration (where the probability of being a
137 temporary emigrant only depends on the status of the individual at a given capture occasion) and a
138 Markovian emigration (where the probability of being a temporary emigrant depends on the status of the
139 individual at a given time step and at the previous time step). We tested 4 possible effects on survival: no
140 effect, a sex effect, an age effect, and an additive effect of sex and age. Finally, 6 possible effects on
141 detection were considered: no effect, a sex effect, a time effect (where the probability of detection changed

142 between primary occasions – years, in our study), a mixture effect (with two distinct classes or individuals to
143 account for detection heterogeneity, e.g. Cubaynes et al. (2010)), and the additive effects of sex and time and
144 sex and mixture. In total, we tested 72 different models (Supplementary materials).

145 We used the Akaike Information Criterion corrected for small sample size (AICc) to perform model selection
146 (Burnham and Anderson 2002). For each dataset (France, Spain, Combined), we kept the models with a
147 AICc weight > 0.01 . We also model-averaged parameter estimates to account for uncertainty in selecting one
148 single ‘best’ model. To obtain 95% confidence intervals on abundance, we used a non-parametric bootstrap
149 in which individual capture histories from each dataset were resampled with replacement a hundred times
150 (Buckland et al. 1997).

151 We used the program MARK (White and Burnham 1999) called from software R (RCoreTeam 2013) with
152 the ‘RMark’ package (Laake 2013).

153 **Results**

154 1. Descriptive statistics

155 7517 bear tracks were gathered in the Pyrenees between 2008 and 2014. The number of tracks that were
156 usable in a robust design framework for the French, Spanish and Combined dataset by both being accurate
157 enough and collected between May and September (see Supplementary data) is shown in Table 1, and
158 amounted for 15 to 17% of the total tracks.

159 2. Model selection with the French dataset

160 The models that were selected for the French dataset mostly included a mixture effect on detection (Table
161 2A), whether alone or with an additive effect of sex. Survival was linked either to no effect, or to an effect of
162 sex. However, no specific type of emigration (none, random or Markovian) was preferentially selected. The
163 three best models (AICc weight > 0.1) included a sex effect along with individual heterogeneity on detection,
164 and no effect on survival. No time effect on detection was found in the best models, and only the 12th best
165 had an age effect on survival.

166 3. Model selection with the Spanish dataset

167 All models selected for the Spanish dataset included emigration, whether it was random or Markovian (Table
168 2B), with the four best-ranked models having a random emigration. Models without emigration had a
169 significantly lower weight. In contrast with the French dataset, the heterogeneity of detection (mixture effect)
170 was seldom kept in the best models. Instead, most of the best models either had no effect or a sex effect for
171 both survival and detection. The four best models (AICc weight >0.08) had a random emigration, and either
172 no effect of a sex effect on both survival and detection.

173 4. Model selection with the Combined dataset

174 Like in the French dataset, all the best models for the Combined dataset had a mixture effect on detection,
175 whether it was alone or with an additive effect of sex (Table 2C). No clear pattern emerged for emigration,
176 although the models with Markovian emigration tended to have a lower weight. The results were similarly
177 contrasted for the effects on survival, with sex being kept in 8 of the 15 models and age in 5 of 15.

178 5. Abundance estimates

179 In Spain, population increased to stabilize around 10 individuals, but showed a steep fall in 2013 before
180 recovering in 2014 (Figure 2), which may indicate individuals that were temporarily unavailable. The French
181 dataset pictured a very small increase between 2008 and 2014. The Combined dataset showed a trend similar
182 to the Spanish dataset, with an increase between 2008 and 2014 and a temporary fall in 2013 mostly due to
183 the lack of individuals detected on the Spanish side of the Pyrenees.

184 6. Demographic parameter estimates

185 The survival estimates were higher in France than in Spain (Table 3). There was a notable difference
186 between male and female survival in the Combined dataset ($F = 0.81 \pm 0.051$, $M = 0.933 \pm 0.041$). In the
187 France and Combined datasets, two classes of individuals were identified detection-wise, with one class
188 being easily detected ($\sim 0.7-0.8$) and one being harder to detect ($\sim 0.3-0.4$). In both cases, the detection
189 probability of females ended up being slightly inferior to the detection probability of males.

190 In the Spain dataset, emigration was much higher than in the other datasets. This might be explained by the
191 very few individuals found in 2013 that were probably treated by the models as temporary emigrating.
192 Moreover, all models selected for the Spain dataset included a random or Markovian emigration, while the

193 France and Combined datasets also selected models with no emigration, which might have lowered the
194 estimated values when averaged.

195 **Discussion**

196 1. Abundance and heterogeneity in the detection process

197 The results for the French and Combined datasets highlighted two classes of individuals with significantly
198 different detection. A previous study on wolves highlighted the importance of individual detection
199 heterogeneity (IDH) when estimating abundance of large carnivore populations (Cubaynes et al. 2010). IDH
200 in the Pyrenean brown bears might stem from intraspecific home range disparities (McLoughlin et al. 2000)
201 making it more likely to find tracks of individuals who move a lot. The individual that was detected the most
202 often, Pyros, is also the male with the highest reproductive success, and the three most commonly seen males
203 (Pyros, Balou and Nere) were the three oldest living males in 2014. Another factor that might cause IDH is
204 the efficiency of human agents when looking for bear tracks. Some Pyrenean bears display a stable spatial
205 behavior over the years (Camarra et al. 2015), making their movements predictable in time. The personality
206 differences displayed by bears (Fagen and Fagen 1996) might allow the agents to become better at finding
207 tracks.

208 2. Sex and age effect on survival

209 A result that was consistent in all datasets was the lack of an age effect on survival. This is unexpected since
210 young bears generally suffer from higher mortality rates (Bunnell and Tait 1985). However, because our
211 analysis only included data ranging from May to September, we excluded the first four or five months of life
212 for the bear cubs, during which their survival rate is at its lowest, meaning that bear cub deaths might have
213 simply gone unnoticed due to the absence of the cubs from the dataset.

214 The presence of an effect of sex on survival, with higher mortality rates for females, seemed to contradict a
215 previous study performed on grizzly bears where mortality was higher among males (McLellan et al. 1999).
216 However, in this study, hunting explained the bias towards male mortality, since death from natural causes
217 was more common among females. Because bear hunting is banned in the Pyrenees, the results between the
218 two studies are actually consistent.

219 3. Estimates of the demographic parameters

220 Female bears survival in the Combined dataset was consistent with previous studies performed in other
221 populations (De Barba et al. 2010; Garshelis et al. 2005; Wielgus and Bunnell 1994). Male bears survival in
222 the same dataset was consistent with a previous study on a population without hunting pressure (De Barba et
223 al. 2010). The emigration rate was significantly higher when using only the Spanish dataset compared to the
224 French and Combined datasets, which could indicate that bears travel more from the Spanish to the French
225 side of the Pyrenees. This important emigration rate on the Spanish side might also result from demographic
226 stochasticity, stemming from the small size of the population and the very low number of individuals
227 identified in Spain in 2013.

228 4. Robust design as a tool to estimate population size for cryptic species

229 Rare populations can either be defined by the low number of individuals, or by the fact that the population
230 belongs to elusive, hard-to-observe species with large home ranges and low density (McDonald 2004). The
231 Pyrenean brown bear population falls under both cases, and as such estimating its demographic parameters is
232 made even more difficult. We confirmed however that robust design capture-recapture models allowed
233 estimating several population parameters (Smith et al. 2013). In our case, the robust design study was
234 combined with the use of multiple data sources (Boulangier et al. 2008; Gervasi et al. 2012) to obtain enough
235 captures so we could build capture-recapture datasets with a sufficient number of observations to be
236 exploited.

237 Abundance estimates were different from those calculated yearly by the GSTOP, which found a significant
238 increase in the minimal population size between 2008 and 2014, going from 17 to 31 individuals (Camarra et
239 al. 2015). This discrepancy can be explained by the method used by the agencies, which use both a Minimal
240 Kept Population Size (EMR) and a Minimal Detected Population Size (EMD). Every year, the EMD can be
241 used to correct the previous year's EMR if some bears were not detected, due to the fact that the population
242 is assumed geographically closed. In comparison, our robust design framework includes temporary
243 emigration, which means that a bear that is not found during an entire year will not be included in the total
244 population size. Moreover, to use the robust design framework, we excluded tracks that were difficult to
245 date, and those that fell outside of the secondary occasions (May to September), which left some individuals

246 identified by the GSTOP (Camarra et al. 2015) out of our database (see Supplementary materials). Agency
247 estimates performed so far always included the individuals that were found dead in their yearly counts
248 (Camarra et al. 2015), while a robust design model would only include them if the death occurred after the
249 end of the primary occasion. Finally, the gender of a single individual born in 2012 was not determined, and
250 as such that bear was excluded from our analyses. These factors put together account for the differences with
251 the counts performed by the GSTOP.

252 5. Implications for bear abundance estimates

253 Even though different methods are used to estimate brown bear population size such as distance sampling
254 and capture-recapture methods (Solberg et al. 2006), once the analyses are performed, most brown bear
255 populations over the world are described by their total number of individuals, whether it is in Italy (Gervasi
256 et al. 2008), in Sweden (Kindberg et al. 2011) or in the USA (Boulanger et al. 2008). Some other carnivore
257 populations, however, are described with different indicators, such as the number of potential family groups
258 (Andren et al. 2002) or the number of females with cubs of the year (Palomero et al. 2007). Considering the
259 importance of the minimum population size for its viability (Shaffer 1981), we suggest that in complement to
260 the minimal population size used by the GSTOP to describe the Pyrenean brown bears, it is important to
261 develop an alternate counting method, especially since the heavy inbreeding (Camarra et al. 2015; Chapron
262 et al. 2009) means that the genetic effective size (Palstra and Ruzzante 2008) of the Pyrenean brown bear
263 population is lower than the “real” population size would let us to believe. Brown bear females in Europe
264 (Swenson et al. 2007) usually start reproducing at the age of 4 or 5 with an interbirth interval of 2 years at
265 least (Schwartz et al. 2003). Therefore, we suggest also describing the population by using the number of
266 females with cubs of the year (Palomero et al. 2007) or the total number of 4+ years old females in the
267 population, instead of limiting ourselves to the total number of bears. This would give a much more accurate
268 insight of the viability of the population, which is an important tool to use when dealing with the
269 conservation of endangered populations (Beissinger and Westphal 1998).

270 6. Importance of transboundary management

271 A transboundary management strategy helps to avoid significant errors in the estimates, most importantly the
272 overestimation that occurs when a single individual is accounted for in one or more political jurisdiction due

273 to its mobility(Bischof et al. 2016). The sum of yearly abundance in France and Spain was always larger than
274 abundance from the Combined dataset, hence confirming this assumption. Even though administrative
275 borders might coincide with a difference in local priorities (Moilanen and Arponen 2011), such as the
276 Scandinavian lynx (*Lynx lynx*) population which is much more heavily hunted in Norway than it is in
277 Sweden (Swenson and Andrén 2005),a transboundary approach allows for more biologically logical
278 management (Linnell and Boitani 2012). Differing management policies between two neighboring
279 jurisdictions can have consequences on a large carnivore population, e.g. by creating source/sink dynamics
280 (Swenson and Andrén 2005)that will in turn affect demography (Robinson et al. 2008). Here, we showed that
281 it was possible to build a transborder model despite differences in monitoring methods between the different
282 jurisdictions.

283 **Conclusion**

284 Perceived errors in abundance estimates might lead to skepticism towards the results provided by scientists,
285 which can be followed by a negative evolution of a conservation conflict (Redpath et al. 2013). While
286 accurate scientific data is not sufficient to solve the contention surrounding some large carnivore
287 populations, it is a necessary step to advance towards mitigating conflicts by allowing the identification of
288 human and ecological impacts (Redpath et al. 2013). It is especially important in the case of the Pyrenean
289 brown bear, where the recent relocation of a male Slovenian bear in Catalonia could lead to an increase of
290 the conflict, playing on the attitude differences between Pyrenean residents (Piédallu et al. 2016). In this
291 context, reliable scientific data will be needed to avoid widening the gap between supporters and opponents
292 of bear presence in the French-Spanish mountains. As large carnivore populations recover in Europe
293 (Chapron et al. 2014), transboundary monitoring, however complex it might be (Kark et al. 2015),could
294 become an essential first step towards harmonious and efficient transboundary management(Bischof et al.
295 2016; Kark et al. 2015), as it will be easier to implement than transboundary policies(Kark et al. 2015), and
296 could facilitate the development of efficient solutions to ingrained conservation conflicts (Redpath et al.
297 2013).

298 **Tables & Figures**

299 **Table 1: Number of bear tracks found yearly**

		2008	2009	2010	2011	2012	2013	2014	Total	%Total Tracks	%ID'd Tracks
	All year	99	58	159	189	228	203	162	1098	22.80%	74.34%
France	May-Sep	80	52	123	130	157	161	121	824	17.11%	55.79%
	Apr-Nov	94	56	154	178	208	199	147	1036	21.52%	70.14%
	All year	37	54	90	145	101	48	93	568	21.02%	63.18%
Spain	May-Sep	24	41	65	124	66	29	77	426	15.77%	47.39%
	Apr-Nov	36	51	80	142	101	48	91	549	20.32%	61.07%
	All year	136	112	249	334	329	251	255	1666	22.16%	70.12%
Total	May-Sep	104	93	188	254	223	190	198	1250	16.63%	52.61%
	Apr-Nov	130	107	234	320	309	247	238	1585	21.09%	66.71%

300

301 Number of bear tracks per primary occasion of capture/Year. Two sets of secondary occasions are depicted:

302 May-Sep (from May to September) and Apr-Nov (from April to November). The Total and Identified

303 number of tracks in each dataset are shown in Table 1 of the Appendix section.

304

305 **Table 2: Model selection for each of the three datasets**

(a) France							
#	Survival	Detection	Emigration	npar	AICc	Weight	Deviance
6	0	Sex + Mix	None	12	649.3	0.27	636.1
30	0	Sex + Mix	Markovian	14	650.2	0.17	632.4
54	0	Sex + Mix	Random	13	651.1	0.11	635.6
12	Sex	Sex + Mix	None	13	651.2	0.10	635.7
28	0	Mix	Markovian	13	651.6	0.08	636.1
4	0	Mix	None	11	652.7	0.05	641.7
60	Sex	Sex + Mix	Random	14	653.1	0.04	635.3
34	Sex	Mix	Markovien	14	653.5	0.03	635.7
52	0	Mix	Random	12	653.8	0.03	640.6
10	Sex	Mix	None	12	654.5	0.02	641.2
26	0	Sex	Markovian	12	655.4	0.01	642.2
18	Age	Sex + Mix	None	19	655.5	0.01	625.9
58	Sex	Mix	Random	13	655.6	0.01	640.2
36	Sex	Sex + Mix	Markovian	15	655.8	0.01	635.7
(b) Spain							
#	Survival	Detection	Emigration	npar	AICc	Weight	Deviance
49	0	0	Random	10	447.8	0.25	420.9
50	0	Sex	Random	11	448.1	0.21	418.9
55	Sex	0	Random	11	449.6	0.10	420.3
56	Sex	Sex	Random	12	450.0	0.08	418.4
25	0	0	Markovian	11	450.1	0.08	420.8
26	0	Sex	Markovian	12	450.5	0.07	418.8
52	0	Mix	Random	12	451.4	0.04	419.7
31	Sex	0	Markovian	12	451.9	0.03	420.3
54	0	Sex + Mix	Random	13	452.3	0.03	418.2
32	Sex	Sex	Markovian	13	452.4	0.03	418.3
58	Sex	Mix	Random	13	453.3	0.02	419.2
28	0	Mix	Markovian	13	453.7	0.01	419.7
(c) Combined							
#	Survival	Detection	Emigration	npar	AICc	Weight	Deviance
12	Sex	Sex + Mix	None	13	725.0	0.21	724.5
6	0	Sex + Mix	None	12	725.2	0.19	726.9
58	Sex	Mix	Random	13	726.2	0.11	725.8
52	0	Mix	Random	12	726.4	0.10	728.1
18	Age	Sex + Mix	None	19	727.6	0.06	713.6
72	Sex + Age	Sex + Mix	Random	21	727.8	0.05	709.1
34	Sex	Mix	Markovian	14	728.4	0.04	725.8
28	0	Mix	Markovian	13	728.5	0.04	728.1
24	Sex + Age	Sex + Mix	None	20	728.6	0.03	712.3
10	Sex	Mix	None	12	728.9	0.03	730.7
64	Age	Mix	Random	19	729.2	0.02	715.3
4	0	Mix	None	11	729.4	0.02	733.3
36	Sex	Sex + Mix	Markovian	15	729.4	0.02	724.5
30	0	Sex + Mix	Markovian	14	729.6	0.02	726.9
70	Sex + Age	Mix	Random	20	730.2	0.02	713.9

306

307 List of the best models (Weight > 0.01) selected for each one of the three datasets ((a) France (b) Spain (c)

308 Total). #: Number of the model. Survival, Detection, Emigration: effects tested on each parameter in the

309 model. 0: No effect on the parameter. npar: number of parameters. Note: whenever model averaging was

310 impossible due to the different nature of the models (with or without a mixture effect), we only selected the
311 category with the highest combined weight.

312 **Table 3: Model-averaged parameter estimates**

Dataset	Bear Class	Survival	Detection	Emigration	Immigration
France	Female class 1	0.90 ± 0.07	0.84 ± 0.13	0.08 ± 0.08	0.50 ± 0.46
	Female class 2		0.36 ± 0.05		
	Male class 1	0.92 ± 0.06	0.88 ± 0.10		
	Male class 2		0.45 ± 0.06		
Spain	Female	0.83 ± 0.06	0.48 ± 0.04	0.27 ± 0.09	0.25 ± 0.14
	Male	0.85 ± 0.07	0.52 ± 0.04		
Total	Female class 1	0.88 ± 0.05	0.73 ± 0.13	0.07 ± 0.05	0.10 ± 0.14
	Female class 2		0.32 ± 0.05		
	Male class 1	0.93 ± 0.04	0.81 ± 0.05		
	Male class 2		0.41 ± 0.06		

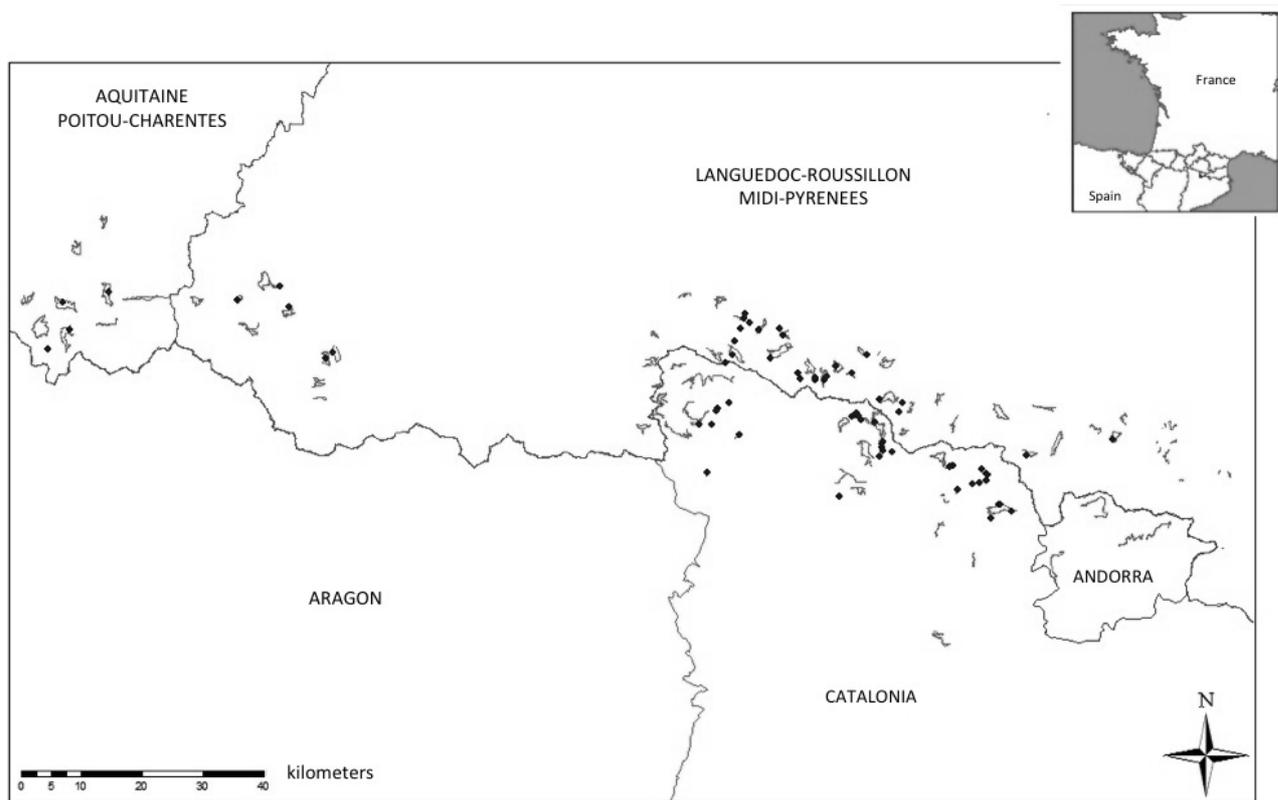
313

314 Model-averaged parameter estimates for each of the datasets. Bear Class represents the different individual

315 classes identified by the mixture effect.

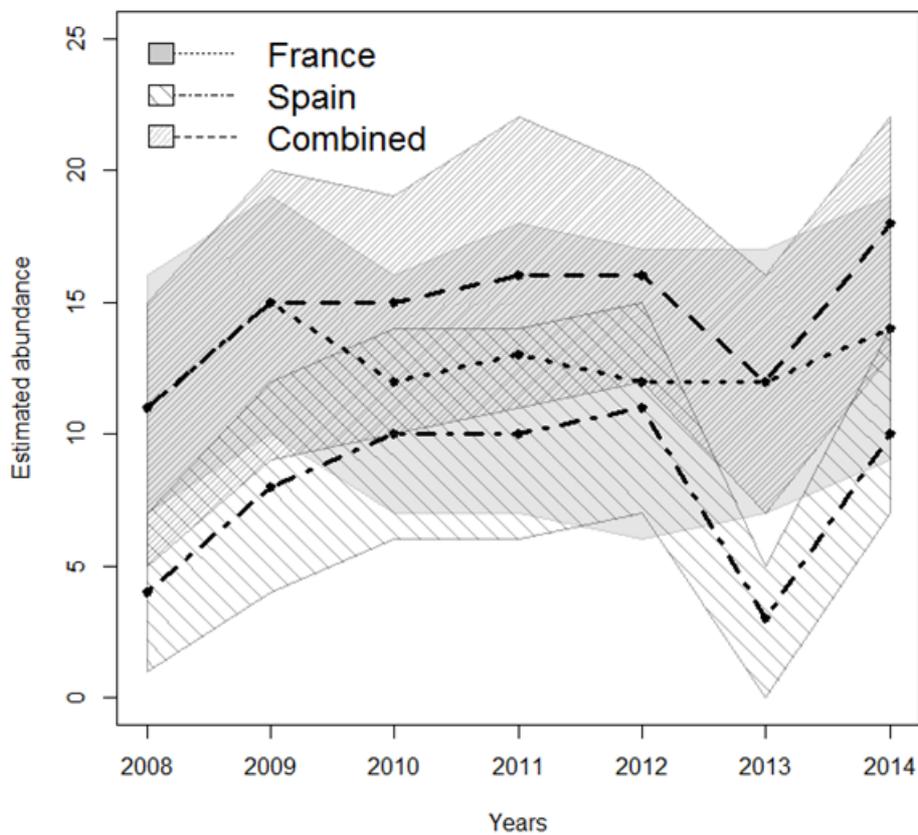
316

317 **Fig. 1: Map of bear monitoring in the French and Spanish Pyrenees**



318
319 Bear monitoring in the French and Spanish Pyrenees. Thin lines: systematic itineraries. Dots: camera traps.
320 The top-right mini-map indicates French counties and Spanish province – only the westernmost French
321 county is part of the Aquitaine-Poitou-Charentes region, all the others are part of the Languedoc-Roussillon-
322 Midi-Pyrénées region. In France, data monitoring is handled by the Game and Wildlife Agency. In Spain,
323 monitoring is handled separately between the three Autonomous communities: in Catalonia, the Fauna and
324 Flora Service of the Department of Territory and Sustainability is in charge with a local delegation to the
325 General Council in the Val d’Aran; in Aragon, it is the Environmental Services Department that oversees
326 bear management, and in Navarre, it is the Public Society for Environmental Management of Navarre. In
327 Andorra, monitoring is handled by the Natural Heritage Department.

328 **Figure 2: Population size estimation for each dataset**



329

330 Population size for the Pyrenean brown bears between 2008 and 2014 estimated using the three different
331 datasets (France only, Spain only, and Combined).

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