1 **Determinants and patterns of the endangered brown bear *Ursus arctos* habitat**
2 **use in the French Pyrenees revealed by occupancy modeling**

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22 **Word count: 5995**

23

24 **Abstract**

25 The Pyrenean brown bear (*Ursus arctos*) in the mountainous border between France and
 26 Spain is one of the smallest and most endangered populations of large carnivores in Europe.
 27 Here, we aimed at assessing trends in brown bear habitat use in the Pyrenees and determining
 28 the underlying environmental and anthropogenic drivers. Using detection/non-detection data
 29 collected between 2008 and 2014 through non-invasive methods, we developed occupancy
 30 models to investigate the dynamic of brown bear habitat use in the Pyrenees accounting for
 31 local colonization and extinction processes. First, we found two non-connected occupancy
 32 cores, one located in the West and another in the Center of the Pyrenees, with an overall
 33 significant decrease in habitat use between 2008 and 2014. Second, we showed a negative
 34 correlation between human density and bear occupancy in agreement with previous studies on
 35 brown bear habitat suitability. Our results confirm the critically endangered status of the
 36 Pyrenean population of brown bears.

37 **Keywords:** dynamic occupancy model, extinction, habitat use, imperfect species detection,
 38 large carnivores, local extinction, *Ursus arctos*

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40

41 **Introduction**

42 Over the last decades, large carnivore populations have been recovering in Europe following
 43 the implementation of conservation policies (Chapron *et al.*, 2014). In parallel, conflicts
 44 surrounding the animals' presence subsist (Treves and Karanth, 2003). More than the direct
 45 danger caused by carnivore presence, the main sources of conflicts are the damage on
 46 livestock and the competition with local hunters (Ericsson and Heberlein, 2003, Gunther *et*
 47 *al.*, 2004, Piédallu *et al.*, 2016a). For these conflicts to be solved or at least mitigated - a
 48 necessary step in the conservation of wild populations - the expectations of all stakeholders
 49 should be considered and the management decisions should be based on solid ecological data
 50 (Redpath *et al.*, 2013).

51 Among the four species in continental Europe is the brown bear *Ursus arctos*, which is
 52 widely distributed all over the continent and split in numerous populations of varying sizes
 53 and ranges (Swenson, Taberlet and Bellemain, 2011), including the large Swedish population
 54 (Kindberg *et al.*, 2011) or the much smaller one living in the Italian Apennines (Gervasi *et al.*,
 55 2012). One of the smallest and most endangered of these populations resides in the Pyrenees
 56 mountains between Southwestern France and Northeastern Spain and is considered to be
 57 critically endangered by the IUCN (Huber, 2007). Its survival required the translocation of
 58 Slovenian individuals in 1996-97, 2006 and 2016 after only five individuals were detected in
 59 1995, and it remains to this day small and threatened by demographic stochasticity and
 60 inbreeding (Chapron *et al.*, 2009, Swenson *et al.*, 2011).

61 The distribution of a wild population is a key element on which the IUCN relies to
 62 determine its conservation status (IUCN, 2012). However, this state variable is difficult to
 63 assess in the case of elusive species with large home ranges (Gittleman and Harvey, 1982),

64 brown bear making no exception. To infer the distribution of large carnivores, their
65 monitoring often relies on tracks and indirect observations coupled with DNA analyses to
66 identify the species (e.g., Bellemain *et al.*, 2005, McDonald, 2004, Taberlet *et al.*, 1997). In
67 the case of the French brown bear, its actual distribution remains poorly studied. Martin *et al.*
68 (2012) conducted habitat suitability analyses at a coarse scale on the Cantabrian brown bear
69 population in Spain and applied it in the Pyrenees, and at a local scale using bear detections in
70 the Pyrenees and presence-only methods. Here, we intend to build on these results to address
71 two main issues in standard species distribution models.

72 First, when dealing with free-ranging populations, species detectability is most likely
73 less than 1, which can lead to false negatives where animals are present but not detected
74 during the survey (Kéry, 2011). Falsely assuming perfect detection can lead to an
75 underestimation of the actual species distribution (Lahoz-Monfort, Guillera-Aroita and
76 Wintle, 2014). Site-occupancy models were specifically developed to explicitly disentangle
77 non-detection from actual absence through the modeling of the imperfect, possibly
78 heterogeneous, observation process (MacKenzie *et al.*, 2002). Second, another limit of
79 standard species distribution models is the assumption that the species always occupy the
80 most favorable area, and that dispersal allows reaching these ideal territories - both statements
81 originating from the ecological niche concept (Leibold, 1995). However, natural barriers or
82 dispersal limitations (such as being an extremely small population) may prevent a species
83 from reaching a favorable area (Araújo and Guisan, 2006). To address this issue, static
84 occupancy models were extended to account for colonization and extinction processes – so-
85 called dynamic or multi-season occupancy models (MacKenzie *et al.*, 2003). Although static
86 occupancy models have often been used on large carnivores (e.g., Bayne, Boutin and Moses,
87 2008, Carroll and Miquelle, 2006, Carroll *et al.*, 2003, Hines *et al.*, 2010), there are only few
88 applications of dynamic occupancy models (Miller *et al.*, 2013, Molinari-Jobin *et al.*, 2012).

89 In this study, we identified environmental or anthropogenic drivers and trend in brown
90 bear habitat use in the French Pyrenees. To do so, we fitted dynamic occupancy models to
91 detection/non-detection data obtained through a multi-source systematic monitoring protocol
92 between 2008 and 2014.

93 **Material & Methods**

94 1. Study area and bear population

95 This study was performed on the French side of the Pyrenees at the border between
96 Northeastern Spain and Southwestern France (Figure 1). The bears that live here mostly
97 descend from individuals that were translocated from Slovenia to the Pyrenees in 1996-1997
98 (2 females and 1 male) and 2006 (4 females and 1 male), even though one bear's mother
99 belonged to the remnant of the original Pyrenean bear population which was thought to
100 include 5 individuals in 1995. Field observations suggest that two population cores exist on
101 the French side of the Pyrenees: two male bears have been accounted for in the Western core,
102 and the Central one accounts for the rest of the population (Figure 1).

103 2. Bear data collection and monitoring

104 The data used for this analysis was gathered between 2008 and 2014 by members of the
105 national Brown Bear Network (135 professional members from government agencies and 228
106 unaffiliated amateur members) under the supervision of the French Game and Wildlife
107 Agency (ONCFS). A systematic monitoring protocol was followed using fixed itineraries
108 along which the agents looked for bear tracks such as hair, scats, claw marks or paw prints.
109 The Pyrenees were broken down in mountain massif subsections using ridgelines and the
110 bottom of valleys. The area of a subsection was 95km² on average. This is coherent with the
111 home range of brown bear males and females that is approximately 85-200km² and 50-
112 100km² respectively (Huber and Roth, 1993, Preatoni *et al.*, 2005). Besides, the upper limits

of these home ranges were obtained over a period including the rut in May-June, while we used in our analyses the July-November period (see next section) during which the size of home ranges are much reduced because the rut is excluded (Preatoni *et al.*, 2005). Each one of the 84 investigated subsections of the mountain massif included one itinerary. Each itinerary was visited at least once every month from July to November. The length of each itinerary was proportional to the area of the corresponding subsection so as to survey 0.2 km per km² of subsection. Tracks and observations were validated by ONCFS experts, therefore minimizing the risk of false positives due to species misidentification (Molinari-Jobin *et al.*, 2012).

3. Model building and selection

To estimate the probability of bear presence in all the mountain massif subsections, we built a dynamic occupancy model (MacKenzie *et al.*, 2003) that was parameterized with the probabilities of colonization γ (the probability for a subsection to become occupied while it was unoccupied the year before), extinction ϵ (the probability for a subsection to become unoccupied while it was occupied the year before) and initial occupancy ψ_1 (the probability for a subsection to be occupied the first year of the study), along with the species detection probability p (the probability to detect the species on a subsection when present). We used years as primary occasions, between which colonization and extinction probabilities could be estimated, and the months of July to November as secondary occasions during which we considered the subsections' occupancy status to remain unchanged (the closure assumption). By focusing on the July-November period, we excluded the reproduction season (April to June) during which male bears in particular are known to increase their movement range while they look for females (Clevenger, Purroy and Pelton, 1990). Despite this precaution, movements may still occur in and out the subsections and, assuming these movements are

random, occupancy should be interpreted as habitat use rather than the proportion of area occupied by the species (MacKenzie and Nichols, 2004). More precisely, “the usage made of various habitat components within the home range” is usually referred to as third-order selection (Johnson, 1980).

We relied on previous habitat suitability studies on brown bears in Europe to select candidate environmental and anthropogenic covariates for our analysis (Martin *et al.*, 2010, Martin *et al.*, 2012, Mertzanis *et al.*, 2008). We considered five environmental and anthropogenic covariates for each mountain massif subsection (Table 1; Figure A1). Roughness was obtained as the mean of the absolute differences between the altitude of a massif subsection and the value of its contiguous mountain subsections (Wilson *et al.*, 2007). We used the IGN BD_ALTI® database (250m resolution) to calculate the mean altitude of each massif subsection. Forest cover and shrub cover covariates were extracted from the CORINE Land Cover® database (U.E – SoeS. Corine Land Cover 2012). Road length was built using the IGN ROUTE 500® database. Human density was obtained from the NASA Socioeconomic data and applications center (<http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-count/data-download>). The maximum correlation between these covariates was 0.51 in absolute value. We used the Akaike’s Information Criterion (AIC, Burnham and Anderson, 2002) for covariate selection. To compare model support with reference to the model best supported by the data, we used the difference in AIC (ΔAIC). To account for model selection uncertainty, we resorted to model averaging considering all models with $\Delta AIC < 2$. Due to the large number of covariate combinations, we used a multi-stage approach to model selection (Dugger, Anthony and Andrews, 2011, Lee and Bond, 2015, MacKenzie *et al.*, 2012), which proceeded as follows. First, we started by selecting the best model structure by focusing on time-varying covariates only, namely *year* and *survey*. We considered 8 different models in total, with either no effect (.) or a *year* effect on colonization

γ and extinction ϵ , and either no effect (.) or a *survey* effect (where a survey refers to a month, hence a survey specific covariate) on detection probability p (Table 2). Because the sampling effort was homogeneous over the study period, we did not consider a *year* effect on detection. Second, based on previous bear occupancy studies (Martin *et al.*, 2010, Martin *et al.*, 2012, Mertzanis *et al.*, 2011, Nielsen *et al.*, 2010, Nielsen, Stenhouse and Boyce, 2006) and bear biology, we considered *specific* combinations of the environmental or anthropogenic effects on each of the parameters (ψ_1 , γ , ϵ and p , Table 1). We tested possible negative effects of covariates human density and road length on initial occupancy ψ_1 as a previous study showed that bears avoided human-caused disturbances (Martin *et al.*, 2010, Mertzanis *et al.*, 2011, Naves *et al.*, 2003). Roughness, shrub cover and forest cover were all positively associated with bear presence albeit performed at different scales in previous studies (Apps *et al.*, 2004, Martin *et al.*, 2010, Martin *et al.*, 2012, Naves *et al.*, 2003, Nellemann *et al.*, 2007). For colonization γ , we studied possible effects of roughness and human density that were the most commonly significant covariates in previous bear distribution studies (Martin *et al.*, 2010). We considered for extinction ϵ the possible effect of the two anthropogenic covariates human density and road length. Finally, we tested the possible effect of human density, roughness and forest cover on detection p as both could potentially influence the accessibility of bear tracks to observers. To account for the variability in the size of a subsection, we also included its area as a covariate on detection in all models without submitting it to selection. In total, we fitted all possible 8192 models.

Because there was uncertainty in the selection of the best set of covariates, we resorted to model-averaging for parameter estimation and inference (Burnham and Anderson, 2002). Effect sizes were examined to determine the magnitude of a covariate effect (Nakagawa and Cuthill, 2007). The covariates were standardized prior to the analyses.

To assess a potential trend over the years in habitat use, we first estimated the occupancy status of each subsection for each year. We then tested a linear effect of year on the binary occupancy variable using a conditional autoregressive correlation model and an adjacency matrix between the different subsections to specify the correlation matrix (Rousset and Ferdy, 2014). A likelihood ratio test (LRT) was performed to assess the significance of this temporal trend. We applied this procedure to all models with $\Delta AIC < 2$.

Eventually, we built maps for initial occupancy, detection, colonization and extinction by calculating the probability at a given subsection using the model-averaged parameter estimates and the value of the covariates for this given subsection.

These analyses were performed in R (RCoreTeam, 2013) with the ‘unmarked’ (Fiske and Chandler, 2011), spaMM (Rousset and Ferdy, 2014), rgdal, AICcmodavg, classInt, RColorBrewer and spdep packages. The data and R codes are available on GitHub at https://github.com/oliviergimenez/ursus_Pyrenees_occupancy.

Results

1. Multi-stage model selection

We found no *year* or *survey* effects on any of the parameters ψ_1 , γ , ϵ or p (Table 2). The ΔAIC of the next two best models (with a *year* effect on extinction ϵ and a *survey* effect on detection p respectively) was >2 , therefore we used the model with constant parameters as the basic structure for the next step. Despite model uncertainty in the results of the selection procedure on environmental and anthropogenic covariates, some covariates were always included in models with $\Delta AIC < 2$ (Table 3): roughness on detection and colonization probabilities and human density on extinction and initial occupancy probabilities.

2. The effect of covariates on parameters

We refined the patterns found in the covariate selection step by examining the effect sizes (on the logit scale; Figure 2). While the effect of roughness on detection probability and that of human density on both extinction and initial occupancy probabilities were confirmed, the colonization probability was not associated with any covariates. We investigated further the links between the covariates and initial occupancy, colonization, extinction and detection probabilities by assessing the shape of these relationships (after back-transformation; Figure 3). An increase in roughness was associated with an increase in the detection probability, while it was more difficult to detect bears (when present) in large subsections. Initial occupancy ψ_1 was strongly negatively correlated with human density (Figure 2B), with the least populated areas being much more likely to be used by bears, just like extinction ϵ was negatively correlated with human density.

3. Distribution maps

The initial occupancy map (Figure 4B) clearly showed two population cores (Western and Central), with the Central Core extending in Southeast Ariège and Southwest Aude and Pyrénées-Orientales (Figure 1). The extinction probability in the East of the Central core was high (Figure 4D), which is consistent with the disappearance of the bears from that area (Camarra *et al.*, 2012), while the colonization probability in the same mountain subsections were close to zero (Figure 4C). Detection was higher in the Central core than it was in the Western core (Figure 4A). The colonization map indicated that the Western population core was more likely to expand to the East, while the Central one was more likely to expand to the West (Figure 4C). These last observations were confirmed by the yearly occupancy maps (Figure 5), which showed a decrease of the occupancy probability in the Eastern parts of the Central population core (Southeast Ariège, Southwest Aude and Pyrénées-Orientales).

Occupancy in the West of the Western population core (Southwest of the Pyrénées-Atlantiques) also decreased while it remained constant in the East of that core (Southeast of the Hautes-Pyrénées). Overall, a decrease in habitat use by the bear between 2008 and 2014 was detected (p -value < 0.01 for all models in Table 3), with no new areas being colonized while others clearly went extinct.

Discussion

1. Environmental and anthropogenic effects on model parameters

Human density had a strong, negative effect on initial occupancy probability ψ , with the least densely populated areas being the most likely to be used by bears. This result confirms previous analyses suggesting that bears tend to live far from the areas with the most intense human activity (Long *et al.*, 2010, Martin *et al.*, 2010). Several factors such as the habituation of the bears to human presence (Wheat and Wilmers, 2016) or the need for female bears to shield themselves from sexual conflict (Steyaert *et al.*, 2016) may mitigate this effect – but the small current size of the Pyrenean brown bear population limits the immediate relevance of these factors as bears tend to disperse further at low densities, lowering the encounter rate of other individuals and for females the risk of sexually selected infanticide (Stoen *et al.*, 2006). These results confirm that anthropogenic effects supersede natural elements when it comes to habitat selection by brown bears (Nellemann *et al.*, 2007).

Contrary to what we were expecting, human density was negatively correlated with the probability of extinction. A possible explanation is the influence of demographic stochasticity in small populations (Gabriel and Bürger, 1992) which gives more weight to extinction events. In our study, human density was lower in the Southeast of Ariège and Southwest of Aude and Pyrénées-Orientales (Figure A1) than it was in the other areas with high occupancy

probability (Figure 4B), and was the place of several local extinction events in years 2010 and 2011 (Camarra *et al.*, 2012).

Finally, we found a positive correlation between the detection probability and roughness. A rougher terrain funneling pathways of bears and humans may explain this pattern. The same funneling effect might explain why signs of bears were easier to detect (when the species was present) in small subsections than in large ones. Overall, species detection was imperfect and estimated below 0.6, therefore confirming the need to correct for it to avoid underestimating occupancy.

2. Brown bear habitat use in the French Pyrenees

The occupancy maps for bears in the Pyrenees clearly showed the existence of two independent population cores, one located in the West and another in the Center of the Pyrenees (Figure 4B, Figure 5). The two cores remained unconnected during the timespan of the study. The dynamics of occupancy over the study period (Figure 5) showed that habitat use significantly decreased overall. In particular, the extinction of the Eastern part of the Central core is consistent with the lack of bear tracks found in Southeast Ariège and Southwest Aude and Pyrénées-Orientales (Figure 1) since 2011 (Camarra *et al.*, 2012). These results demonstrate the usefulness of dynamic occupancy models to highlight trends in habitat use that cannot be identified by static species distribution models (MacKenzie *et al.*, 2003).

The fact that we found many mountain subsections with a high occupancy probability in the Western core despite the fact that only 2 to 3 bears were estimated to live there between 2008 and 2014 (Piédallu *et al.*, 2016b) suggests a violation of the closure assumption between our secondary occasions (July-November), because there were not enough bears in the population core to occupy all subsections at the same time. This means that we estimated the habitat use by brown bears instead of the actual occupancy. For species that can attack livestock,

presence does not have to be permanent to be a source of conflict, and therefore habitat use remains a relevant indicator in the case of large carnivores often characterized by their relatively large home ranges (Gittleman and Harvey, 1982) and their use of large areas without actually occupying much land at any given time.

3. Implications for human-wildlife conflict mitigation

We anticipate that our results will be useful as part of the “scientific evidence gathering” that is required for conflict mitigation (Redpath *et al.*, 2013). Attacks on livestock are one of the main causes of the negative attitudes towards carnivore presence in general (Kaczensky, Blazic and Gossow, 2004, Sponarski *et al.*, 2013) and towards brown bears in the Pyrenees in particular (Piédallu *et al.*, 2016a). There is an interest in mapping the areas which are more likely to host bears in the present and the future, and as such the “attack hotspots” (Miller, 2015). It could also be combined with a mapping of attitudes towards brown bears (Piédallu *et al.*, 2016a) to identify areas that combine positive attitudes towards bear presence and low attack risk, and as such could be primary targets of future management decisions. This might be the first step towards the development of socio-ecological models designed to mitigate human-wildlife conflicts (Aswani, 2011, Dupont *et al.*, 2011, Estoque and Murayama, 2014).

Acknowledgments

We are grateful to the volunteers of the Brown Bear Network and the ONCFS Bear Team for collecting and sharing precious data and knowledge on the Pyrenean brown bears.

References

- Apps, C. D., McLellan, B. N., Woods, J. G., Proctor, M. F. (2004). Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management* 68, 138-152.
- Araújo, M. B. , Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33, 1677-1688.
- Aswani, S. (2011). Socioecological approaches for combining ecosystem-based and customary management in Oceania. *Journal of Marine Biology* 2011, 1-13.
- Bayne, E. M., Boutin, S., Moses, R. A. (2008). Ecological factors influencing the spatial pattern of Canada lynx relative to its southern range edge in Alberta, Canada. *Canadian Journal of Zoology* 86, 1189-1197.
- Bellemain, E., Swenson, J. E., Tallmon, D., Brunberg, S., Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. *Conservation Biology* 19, 150-161.
- Burnham, K. P. Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. New York: Springer-Verlag.
- Camarra, J. J., Sentilles, J., Bombillon, N. , Quenette, P. Y. (2012). Suivi de l'ours brun dans les Pyrénées françaises. Rapport annuel. Office National de la Chasse et de la Faune Sauvage. URL: http://www.oncfs.gouv.fr/IMG/pdf/Rapport_du_Reseau_Ours_Brun_2012-2.pdf. Last accessed September 16, 2016.
- Carroll, C. , Miquelle, D. G. (2006). Spatial viability analysis of Amur tiger *panthera tigris altaica* in the Russian Far East: The role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology* 43, 1056-1068.

- 325 Carroll, C., Phillips, M. K., Schumaker, N. H. , Smith, D. W. (2003). Impacts of landscape
326 change on wolf restoration success: Planning a reintroduction program based on static
327 and dynamic spatial models. *Conservation Biology* 17, 536-548.
- 328 Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andren, H., Lopez-
329 Bao, J. V., Adamec, M., Alvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P.,
330 Bego, F., Blanco, J. C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci,
331 P., Dutsov, A., Engleder, T., Fuxjager, C., Groff, C., Holmala, K., Hoxha, B.,
332 Iliopoulos, Y., Ionescu, O., Jeremic, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I.,
333 Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majic,
334 A., Mannil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K.,
335 Mertzanis, Y., Myslajek, R. W., Nowak, S., Odden, J., Ozolins, J., Palomero, G.,
336 Paunovic, M., Persson, J., Potocnik, H., Quenette, P. Y., Rauer, G., Reinhardt, I.,
337 Rigg, R., Ryser, A., Salvatori, V., Skrbinek, T., Stojanov, A., Swenson, J. E.,
338 Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Vana, M., Veeroja, R.,
339 Wabakken, P., Wofl, M., Wofl, S., Zimmermann, F., Zlatanova, D. , Boitani, L.
340 (2014). Recovery of large carnivores in Europe's modern human-dominated
341 landscapes. *Science* 346, 1517-1519.
- 342 Chapron, G., Wielgus, R., Quenette, P. Y. , Camarra, J. J. (2009). Diagnosing mechanisms of
343 decline and planning for recovery of an endangered brown bear (*Ursus arctos*)
344 population. *PloS one* 4, e7568.
- 345 Clevenger, A. P., Purroy, F. J. , Pelton, M. R. (1990). Movement and activity patterns of a
346 European brown bear in the Cantabrian Mountains, Spain. *Int. Conf. Bear Res. and*
347 *Manage.* 8, 205-211.

348 Dugger, K. M., Anthony, R. G. , Andrews, L. S. (2011). Transient dynamics of invasive
349 competition: Barred Owls, Spotted Owls, habitat, and the demons of competition
350 present. *Ecological Applications* 21, 2459-2468.

351 Dupont, H., Mihoub, J. B., Becu, N. , Sarrazin, F. (2011). Modelling interactions between
352 scavenger behaviour and farming practices: Impacts on scavenger population and
353 ecosystem service efficiency. *Ecological Modelling* 222, 982-992.

354 Ericsson, G. , Heberlein, T. A. (2003). Attitudes of hunters, locals, and the general public in
355 sweden now that the wolves are back. *Biological Conservation* 111, 149-159.

356 Estoque, R. C., Murayama, Y. (2014). Social–ecological status index: A preliminary study of
357 its structural composition and application. *Ecological Indicators* 43, 183-194.

358 Fiske, I., Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of
359 wildlife occurrence and abundance. *Journal of Statistical Software* 43, 1-23.

360 Gabriel, W., Bürger, R. (1992). Survival of small populations under demographic
361 stochasticity. *Theoretical Population Biology* 41, 44-71.

362 Gervasi, V., Ciucci, P., Boulanger, J., Randi, E., Boitani, L. (2012). A multiple data source
363 approach to improve abundance estimates of small populations: The brown bear in the
364 Apennines, Italy. *Biological Conservation* 152, 10-20.

365 Gittleman, J. L., Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and
366 ecology. *Behavioral Ecology and Sociobiology* 10, 57-63.

367 Gunther, K. A., Haroldson, M. A., Frey, K., Cain, S. L., Copeland, J. (2004). Grizzly bear-
368 human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* 15, 10-22.

369 Hines, J. E., Nichols, J. D., Royle, J. A., MacKenzie, D. I., Gopalaswamy, A. M., Samba
370 Kumar, N. , Karanth, K. U. (2010). Tigers on trails: Occupancy modeling for cluster
371 sampling. *Ecological Applications* 10, 1456-1466.

372 Huber, D. (2007). *Ursus arctos* - The IUCN Red List of threatened species.

373 <http://www.iucnredlist.org/details/41688/1>. Last accessed September 16, 2016.

374 Huber, D., Roth, H. U. (1993). Movements of european brown bears in croatia. *Acta*

375 *Theriologica* 38, 151–159.

376 Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating

377 resource preference. *Ecology* 61, 65-71.

378 Kaczensky, P., Blazic, M. , Gossow, H. (2004). Public attitudes towards brown bears (*Ursus*

379 *arctos*) in Slovenia. *Biological Conservation* 118, 661-674.

380 Kéry, M. (2011). Towards the modelling of true species distributions. *Journal of*

381 *Biogeography* 38, 617-618.

382 Kindberg, J., Swenson, J. E., Ericsson, G., Bellemain, E., Miquel, C., Taberlet, P. (2011).

383 Estimating population size and trends of the Swedish brown bear *Ursus arctos*

384 population. *Wildlife Biology* 17, 114-123.

385 Lahoz-Monfort, J. J., Guillera-Aroita, G., Wintle, B. A. (2014). Imperfect detection impacts

386 the performance of species distribution models. *Global Ecology and Biogeography* 23,

387 504-515.

388 Lee, D. E., Bond, M. L. (2015). Previous year's reproductive state affects Spotted Owl site

389 occupancy and reproduction responses to natural and anthropogenic disturbances. *The*

390 *Condor* 117, 307-319.

391 Leibold, M. A. (1995). The niche concept revisited: Mechanistic models and community

392 context. *Ecology* 76, 1371-1382.

393 Long, R. A., Donovan, T. M., MacKay, P., Zielinski, W. J., Buzas, J. S. (2010). Predicting

394 carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape*

395 *Ecology* 26, 327-340.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2348-2355.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.

MacKenzie, D. I., Nichols, J. D. (2004). Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation* 27, 461-467.

MacKenzie, D. I., Seamans, M. E., Gutiérrez, R. J., Nichols, J. D. (2012). Investigating the population dynamics of California Spotted Owls without marked individuals. *Journal of Ornithology* 152, 597-604.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., Swenson, J. E. (2010). Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* 88, 875-883.

Martin, J., Revilla, E., Quenette, P.-Y., Naves, J., Allainé, D., Swenson, J. E. (2012). Brown bear habitat suitability in the Pyrenees: Transferability across sites and linking scales to make the most of scarce data. *Journal of Applied Ecology*, 49, 621-631.

McDonald, L. L. (2004). Sampling rare populations. In *Sampling rare and elusive species*: 11-42. Thompson, W. L. (Ed.). Washington, DC: Island Press.

Mertzanis, G., Kallimanis, A.S., Kanellopoulos, N., Sgardelis, S.P., Tragos, A., Aravidis, I. (2008). Brown bear (*Ursus arctos*) habitat use patterns in two regions of northern Pindos, Greece – management implications. *Journal of Natural History*, 42, 301–315.

Miller, D. A., Nichols, J. D., Gude, J. A., Rich, L. N., Podruzny, K. M., Hines, J. E. , Mitchell, M. S. (2013). Determining occurrence dynamics when false positives occur:

420 Estimating the range dynamics of wolves from public survey data. *PloS one* 8,
421 e65808.

422 Miller, J. R. B. (2015). Mapping attack hotspots to mitigate human–carnivore conflict:
423 Approaches and applications of spatial predation risk modeling. *Biodiversity and*
424 *Conservation* 24, 2887-2911.

425 Molinari-Jobin, A., Kéry, M., Marboutin, E., Molinari, P., Koren, I., Fuxjäger, C.,
426 Breitenmoser-Würsten, C., Wölfl, S., Fasel, M., Kos, I., Wölfl, M., Breitenmoser, U.,
427 Gompper, M. , Ewers, R. (2012). Monitoring in the presence of species
428 misidentification: The case of the Eurasian lynx in the Alps. *Animal Conservation* 15,
429 266-273.

430 Nakagawa, S., and Cuthill, I. C. (2007). Effect size, confidence interval and statistical
431 significance: A practical guide for biologists. *Biological Reviews* 82, 591–605.

432 Naves, J., Wiegand, T., Revilla, E. , Delibes, M. (2003). Endangered species constrained by
433 natural and human factors: The case of brown bears in northern Spain. *Conservation*
434 *Biology* 17, 1276-1289.

435 Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto,
436 J., Kaltenborn, B. P., Martin, J., Ordiz, A. (2007). Terrain use by an expanding brown
437 bear population in relation to age, recreational resorts and human settlements.
438 *Biological Conservation* 138, 157-165.

439 Nielsen, S. E., McDermid, G., Stenhouse, G. B., Boyce, M. S. (2010). Dynamic wildlife
440 habitat models: Seasonal foods and mortality risk predict occupancy-abundance and
441 habitat selection in grizzly bears. *Biological Conservation* 143, 1623-1634.

442 Nielsen, S. E., Stenhouse, G. B., Boyce, M. S. (2006). A habitat-based framework for grizzly
443 bear conservation in Alberta. *Biological Conservation* 130, 217-229.

444 Piédallu, B., Quenette, P.-Y., Mounet, C., Lescureux, N., Borelli-Massines, M., Dubarry, E.,
445 Camarra, J.-J., Gimenez, O. (2016a). Spatial variation in public attitudes towards
446 brown bears in the French Pyrenees. *Biological Conservation* 197, 90-97.

447 Piédallu, B., Quenette, P. Y., Afonso, I., Bombillon, N., Gastineau, A., Jato, R., Miquel, C.,
448 Muñoz, P., Palazón, S., Solà de la Torre, J., Gimenez, O. (2016b). Better together: A
449 transboundary approach to brown bear monitoring in the pyrenees. Submitted to
450 *Biodiversity and Conservation*. Preprint available from BioRxiv
451 biorxiv.org/content/early/2016/09/16/075663; doi: <http://dx.doi.org/10.1101/075663>.

452 Preatoni, D., Mustoni, A., Martinoli, A., Carlini, E., Chiarenzi, B., Chiozzini, S., Van
453 Dongen, S., Wauters, L. A., Tosi, G. (2005). Conservation of brown bear in the Alps:
454 Space use and settlement behavior of reintroduced bears. *Acta Oecologica* 28, 189–
455 197.

456 RCoreTeam (2013). R: A language and environment for statistical computing.): R Foundation
457 for Statistical Computing.

458 Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A.,
459 Amar, A., Lambert, R. A., Linnell, J. D., Watt, A., Gutierrez, R. J. (2013).
460 Understanding and managing conservation conflicts. *Trends in Ecology & Evolution*
461 28, 100-109.

462 Rousset, F. , Ferdy, J.-B. (2014). Testing environmental and genetic effects in the presence of
463 spatial autocorrelation. *Ecography* 37, 781-790.

464 Sponarski, C. C., Semeniuk, C., Glikman, J. A., Bath, A. J. , Musiani, M. (2013).
465 Heterogeneity among rural resident attitudes toward wolves. *Human Dimensions of*
466 *Wildlife* 18, 239-248.

467 Steyaert, S. M., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J. E.,
468 Zedrosser, A. (2016). Human shields mediate sexual conflict in a top predator.
469 *Proceedings of the Royal Society B: Biological Sciences* 283, 1833.

470 Stoen, O. G., Zedrosser, A., Saebo, S., Swenson, J. E. (2006). Inversely density-dependent
471 natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148, 356-364.

472 Swenson, J. E., Taberlet, P. , Bellemain, E. (2011). Genetics and conservation of european
473 brown bears *Ursus arctos*. *Mammal Review* 41, 87-98.

474 Taberlet, P., Camarra, J. J., Griffin, S., Uhrès, E., Hanotte, O., Waits, L. P., Dubois-Paganon,
475 C., Burke, T. , Bouvet, J. (1997). Noninvasive genetic tracking of the endangered
476 Pyrenean brown bear population. *Molecular Ecology* 6, 869-876.

477 Treves, A. , Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore
478 management worldwide. *Conservation Biology* 17, 1491-1499.

479 Wheat, R. E. , Wilmers, C. C. (2016). Habituation reverses fear- based ecological effects in
480 brown bears (*Ursus arctos*). *Ecosphere* 7.

481 Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., Grehan, A. J. (2007). Multiscale
482 terrain analysis of multibeam bathymetry data for habitat mapping on the continental
483 slope. *Marine Geodesy* 30, 3-35.

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Biographical sketches Blaise Piédallu is a population ecologist interested in human-wildlife conflicts with a focus on large carnivores. Pierre-Yves Quenette is an ecologist who leads the ONCFS brown bear program. Nicolas Bombillon is an ecologist interested in wildlife conservation. Adrienne Gastineau is an ecologist interested in the behavior of large carnivores. Christian Miquel is a population geneticist interested in promoting non-invasive monitoring methods. Olivier Gimenez is a biostatistician interested in population dynamics of large carnivores.

502

503 **Tables & Figures**

504 **Table 1:** Definition of the environmental variables used for the occupancy analysis, and the
 505 parameters for which an effect was tested. ψ_1 : initial occupancy probability, γ : colonization
 506 probability, ϵ : extinction probability, p : detection probability. +/-: predicted sign of the effect
 507 of the covariate on the parameter based on previous studies (see text for references). An
 508 absence of a +/- sign means that the effect was not tested.

Variable name	Description	ψ_1	γ	ϵ	p
Roughness	Mean of the difference between the altitude of a cell and those of all surrounding cells	+	+		-
Forest cover	Percentage of forest cover	+	+		-
Shrub cover	Percentage of shrub cover	+			
Road length	Total length of roads	-		+	
Human density	Average human density	-	-	+	-
Area	Area of subsection				-

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511 **Table 2:** Model selection with time-varying covariates. Models were ranked with AIC. ψ_1 :
512 initial occupancy probability, γ : colonization probability, ϵ : extinction probability, p :
513 detection probability. *year*: year effect on the parameter, which relates to changes between
514 primary occasions, i.e. from one year to another in our case. *survey*: survey effect on the
515 parameter, which relates to the secondary occasions repeated within a year. Δ AIC: difference
516 between the AIC of the current model and the AIC of the model with lowest AIC.

#	Model	AIC	Δ AIC
1	$\psi_1(.) \gamma(.) \epsilon(.) p(.)$	577.1	0
2	$\psi_1(.) \gamma(.) \epsilon(year) p(.)$	581.0	3.9
3	$\psi_1(.) \gamma(.) \epsilon(.) p(survey)$	581.8	4.7
4	$\psi_1(.) \gamma(.) \epsilon(year) p(survey)$	584.5	7.4
5	$\psi_1(.) \gamma(year) \epsilon(.) p(.)$	584.5	7.4
6	$\psi_1(.) \gamma(year) \epsilon(.) p(survey)$	588.0	10.9
7	$\psi_1(.) \gamma(year) \epsilon(year) p(.)$	588.8	11.7
8	$\psi_1(.) \gamma(year) \epsilon(year)$ $p(survey)$	592.3	15.2

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519 **Table 3:** Model selection with environmental and anthropogenic covariates. The covariates
 520 and their combinations are detailed in Table 1. Among the 8192 models that we fitted, we
 521 only report models with $\Delta AIC < 2$. DTHM is for human density, RUG is for roughness,
 522 CVFR is for forest cover, LGRT is for road length, CVBS is for shrub cover. Note that the
 523 area of subsections was used in all models in the detection probability and not subject to the
 524 covariate selection procedure.

Model				AIC
Initial	Colonization	Extinction	Detection	
DTHM	RUG	DTHM + LGRT	RUG	542.0
DTHM	RUG	DTHM + LGRT	RUG + DTHM	542.2
DTHM	RUG	DTHM + LGRT	RUG + CVFR	542.5
DTHM + LGRT	RUG	DTHM	RUG	542.6
DTHM	RUG	DTHM	RUG	542.7
DTHM	RUG + DTHM	DTHM + LGRT	RUG	542.8
DTHM	RUG	DTHM + LGRT	RUG + DTHM + CVFR	542.8
DTHM + LGRT	RUG	DTHM	RUG + CVFR	543.0
DTHM + LGRT	RUG	DTHM	RUG + DTHM	543.0
DTHM	RUG	DTHM	RUG + CVFR	543.2
DTHM + LGRT	RUG	DTHM + LGRT	RUG	543.2
DTHM + LGRT	RUG	DTHM + LGRT	RUG + DTHM	543.2
DTHM	RUG + DTHM	DTHM + LGRT	RUG + CVFR	543.3
DTHM	RUG + CVFR	DTHM + LGRT	RUG	543.4
DTHM + LGRT	RUG	DTHM	RUG + DTHM + CVFR	543.4
DTHM	RUG + DTHM	DTHM	RUG	543.5
DTHM + LGRT	RUG + DTHM	DTHM	RUG	543.5
DTHM	RUG	DTHM	RUG + DTHM	543.5
DTHM	RUG + CVFR	DTHM + LGRT	RUG + DTHM	543.6
DTHM + CVBS	RUG	DTHM + LGRT	RUG	543.6
DTHM + RUG	RUG	DTHM + LGRT	RUG + DTHM	543.6
DTHM	RUG + DTHM	DTHM + LGRT	RUG + DTHM	543.7
DTHM + LGRT	RUG	DTHM + LGRT	RUG + CVFR	543.7
DTHM + RUG	RUG	DTHM + LGRT	RUG	543.8
DTHM + LGRT	RUG	DTHM + LGRT	RUG + DTHM + CVFR	543.8
DTHM + CVBS	RUG	DTHM + LGRT	RUG + DTHM	543.9
DTHM + CVFR	RUG	DTHM + LGRT	RUG	543.9
DTHM	RUG + CVFR	DTHM + LGRT	RUG + CVFR	544.0
DTHM	RUG + DTHM	DTHM	RUG + CVFR	544.0
DTHM + LGRT	RUG + CVFR	DTHM	RUG	544.0

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529 **Figure 1:** Map of the counties and mountain subsections in the French Pyrenees. Dark lines:
530 county borders. Gray lines: limits between mountain subsections.

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Figure 2: Model-averaged parameter estimates (on the logit scale) and confidence intervals of the (standardized) covariates effects on initial occupancy, colonization, extinction and detection probabilities. An effect does not appear if the corresponding covariate was not considered in the selection procedure. The covariates and their combinations are detailed in Table 1: Int. is for the intercept, DTHM is for human density, RUG is for roughness, CVFR is for forest cover, LGRT is for road length, CVBS is for shrub cover and AREA is for the area of subsections. Note that AREA was used in all models in the detection probability and not subject to the covariate selection procedure.

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543 **Figure 3:** Relationships between model-averaged parameter estimates and standardized
544 covariates. We focused on the most important covariates based on the effect sizes given in
545 Figure 2. The parameter of interest is on the y-axis, namely initial occupancy, extinction and
546 detection probabilities. The colonization probability is not displayed because of small effect
547 sizes (we refer to Figure A2 for the relationships between parameters and all covariates). For
548 each relationship, the non-focal covariates were set at their mean. The dashes on the x-axis
549 indicate the observed covariate values.

Figure 4: Maps of the model parameters in the various mountain subsections of the French Pyrenees obtained using the model-averaged parameter estimates. A: Detection probability, B: Initial occupancy probability, C: Colonization probability, D: Extinction probability. Covariates were set at their mean.

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559 **Figure 5:** Maps of the yearly occupancy probability ψ_t from $t = 2008$ to $t = 2014$ in the
560 various mountain subsections of the French Pyrenees obtained using the model-averaged
561 parameter estimates and the formula $\psi_{t+1} = (1-\psi_t) \gamma + \psi_t (1-\epsilon)$ (MacKenzie *et al.*, 2002).
562 Covariates were set at their mean.

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564 **Supplementary materials**

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566 **Figure A1:** Maps of the five environmental or anthropogenic covariates in the mountain
567 subsections of the Pyrenees that were used to build the occupancy models (see also Table 1).

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570 **Figure A2:** Relationships between model-averaged parameter estimates and standardized
571 covariates. A1-A5 is for initial occupancy, B1-B3 for colonization, C1-C2 for extinction and
572 D1-D4 for detection. For each relationship, the non-focal covariates were set at their mean.
573 The dashes on the x-axis indicate the observed covariate values.