







1 **The method matters. A comparative study of biologging and camera traps as data**
2 **sources with which to describe wildlife habitat selection.**

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15

Abbreviations:

RSF: resource selection functions combined with biologging-derived data.

IDM: imperfect detection models coupled with camera trap data.

DNP: Doñana National Park.

BR: Biological Reserve.

CR: Calibration Region.

dwat: Euclidean distance (km) to the nearest artificial water hole.

dvera: Euclidean distance (km) to the nearest marsh–shrub ecotone.

v1: Proportion of dense scrub dominated by *Erica scoparia* and *Pistacia lentiscus*.

v2: Proportion of low-clear shrubland, composed mainly of *Halimium halimifolium*, *Ulex minor* and *Ulex australis*.

v3: Proportion of herbaceous grassland.

v4: Proportion of *Eucaliptus* sp. and *Pinus* sp. Woodland.

v5: Proportion of bare land, sandy dunes and beaches.

v6: Proportion of watercourse vegetation covered mainly by *Juncus* sp. Patches.

time: Sampling occasions of five days, the occasion date.

year: Period date, in this case 2015 or 2016.

typeuse: Type of land use that predominates at the sampling point.

16 **Abstract**

17 Habitat use is a virtually universal activity among animals and is highly relevant as regards
18 designing wildlife management and conservation actions. This has led to the development of a
19 great variety of methods to study it, of which resource selection functions combined with
20 biologging-derived data (RSF) is the most widely used for this purpose. However this approach
21 has some constraints, such as its invasiveness and high costs. Analytical approaches taking into
22 consideration imperfect detection coupled with camera trap data (IDM) have, therefore,
23 emerged as a non-invasive cost-effective alternative. However, despite the fact that both
24 approaches (RSF and IDM) have been used in habitat selection studies, they should also be
25 comparatively assessed. The objective of this work is consequently to assess them from two
26 perspectives: explanatory and predictive. This has been done by analyzing data obtained from
27 camera traps (60 sampling sites) and biologging (17 animals monitored: 7 red deer *Cervus*
28 *elaphus*, 6 fallow deer *Dama dama* and 4 wild boar *Sus scrofa*) in the same periods using IDM
29 and RSF, respectively, in Doñana National Park (southern Spain) in order to explain and predict
30 habitat use patterns for three studied species. Our results showed discrepancies between the
31 two approaches, as they identified different predictors as being the most relevant to determine
32 species intensity of use, and they predicted spatial patterns of habitat use with a contrasted level
33 of concordance, depending on species and scale. Given these results and the characteristics of
34 each approach, we suggested that although partly comparable interpretations can be obtained
35 with both approaches, they are not equivalent but rather complementary. The combination of
36 data from biologging and camera traps would, therefore, appear to be suitable for the
37 development of an analytical framework with which to describe and characterise the habitat
38 use processes of wildlife.

39 **KEYWORDS:** N-mixture models, resource selection functions, imperfect detection models,
40 Doñana National Park, habitat use, wild ungulates.

41 1. INTRODUCTION

42 Habitat use is an almost universal activity among animals and affects all of the individuals'
43 choices and movement parameters (Begon et al., 2006; Manly et al., 2002). Its evident
44 relevance has led considerable attention to be paid to both establishing a theoretical framework
45 for habitat use studies and describing the ways in which organisms of different taxa actually
46 evaluate and select from available habitats (Cody, 1981). One of the main conceptual bases of
47 habitat use studies is that organisms should respond positively to environments in which their
48 survival and reproductive success are higher (Levins, 1968; Orians, 1980). However, it is often
49 difficult to establish correlations between habitat features and animals' fitness in real-world
50 situations, since they are the result of multiple biotic and abiotic interactive factors that should
51 be disentangled from individual/population monitoring data.

52 Biologging is (in a broad sense) the approach most frequently used to describe the habitat use
53 patterns of wildlife (for a review, see Wilmers et al., 2015). Biologging consists of collecting
54 remote data concerning free-ranging animals by using attached electronic devices (Cooke et
55 al., 2004). This provides valuable information on the animals' movements and behaviour,
56 which is very useful as regards understanding their spatial use and habitat selection patterns
57 (Miller et al., 2010; Mulero-Pázmány et al., 2015). Biologging is, therefore, usually combined
58 with resource selection functions in order to study habitat use patterns (Gillies et al., 2006).
59 Briefly, the objective of these functions is to identify and parameterize the differences (in
60 environmental terms) between animals' locations (*used*) and their *availability* in the area
61 (Gillies et al., 2006; Manly et al., 2002). However, biologging still has some constraints, which
62 are principally related to: i) its invasiveness, since it is necessary to capture animals, which
63 requires a relevant sampling effort and could also potentially affects the animals' behaviour,
64 and ii) its expensiveness, signifying that the budgets of most of research projects allow only a
65 reduced number of animals to be monitored (Miller et al., 2010; Recio et al., 2011).

66 Camera traps are a non-invasive sampling method with a huge potential in wildlife monitoring
67 (Burton et al., 2015; Iannarilli et al., 2021; O’Connell et al., 2011; Steenweg et al., 2017). They
68 consist of automatically-trigger cameras that allow to collect photographic evidence of
69 presence of animals in determined sites (Rovero et al., 2010; O’Connell et al., 2011). When
70 non-invasive camera traps are coupled with statistical models that take into account imperfect
71 detection, the result is a cost-effective alternative to biologging with which to study habitat use
72 patterns (MacKenzie et al., 2002), assuming that the fitness of a species (dictated by habitat
73 features) is correlated with population density (Boyce et al., 2016). These models, when
74 employed in a hierarchical framework, use data obtained from sequential repeated (remote
75 camera) surveys to generate probabilities of detection and to produce reliable estimates of the
76 species’ occupancy and abundance, in addition to determining the main drivers of these
77 patterns (Kelly & Holub, 2008; MacKenzie & Royle, 2005; Royle, 2004). Nevertheless, camera
78 traps have some constraints too: i) the time spent in processing photographic images (Jiménez
79 et al., 2017; but see Delisle et al., 2021), the fact that data can only be obtained when animals
80 are active, missing inactivity periods (Gould et al., 2019), and, when combined with N-mixture
81 models, inability to know the effective sampling area of cameras (Gilbert et al., 2021).

82 Resource selection functions coupled with biologging data (hereafter denominated as the RSF
83 approach), and imperfect detection models coupled with camera traps (hereafter denominated
84 as the IDM approach) have been used together in various studies to, for example, describe
85 population dynamics (Duquette et al., 2014), assess the transferability of inferences from the
86 individual to the population level (Bassing et al., 2022) or design biological corridors (Meyer
87 et al., 2020), among others. These approaches have been also used separately in order to
88 describe wildlife habitat use (e.g. Goulart et al., 2009; Schofield et al., 2009; but see Coleman
89 et al., 2014), although few comparative studies exploring the equivalence of the patterns
90 described have been carried out (but see Bassing et al., 2022). However, it should be borne in

91 mind that these approaches are based on two quite different sampling strategies, since
92 biologging usually collects a lot of information from a few individuals (individual scale), while
93 camera trapping collects (usually random) information from the different individuals present
94 in specific points (population scale), so the first is limited with the number of individuals
95 marked, and the second limited with the number of sites sampled. In addition, one must also
96 be aware that the analytical processes are different, where resource selection functions analyse
97 habitat use based on individual animals, while N-mixture models analyse the relative
98 abundance of each site and associate it with habitat predictors. In both approaches, the obtained
99 predictions can be interpreted as intensity of habitat use.

100 In this context, the objective of this study was to compare RSF and IDM when used in order to
101 carry out wildlife studies on habitat use patterns. We have specifically worked with three
102 highly-mobile mammal species: red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild
103 boar (*Sus scrofa*), and assessed whether both approaches are able to: i) identify the main
104 environmental gradients explaining species intensity of habitat use and ii) produce spatial
105 patterns of intensity of habitat use. Our hypothesis is that the inherent peculiarities of each
106 approach (i.e. sampling and analytical differences) should lead to a description of habitat use
107 on a different scale and that the results obtained after employing the two approaches will not,
108 therefore, be equivalent.

109

110 **2. MATERIAL AND METHODS**

111 *2.1 Study Area*

112 The study was performed in Doñana National Park (hereafter, DNP; 37° 08' N; 6° 47' W), a
113 nature reserve located on the Atlantic coast of South-Western Spain (Figure 1). DNP has a total
114 area of 54,252 ha, and hosts a variety of ecosystems including marshlands, lagoons, scrub

115 woodland, forests and sand dunes, which has led to its declaration as a World Heritage Site and
116 Biosphere Reserve (UNESCO 2014). This environmental heterogeneity maintains a great
117 biodiversity. The group of wild ungulates in DNP includes a moderate density of red deer (6.3
118 individuals/100 ha, standard deviation [SD] 1.48) and fallow deer (3.9 individuals/100 ha, SD
119 0.99) and a moderately-high density of wild boar (5.7 individuals/100 ha, SD 1.18) (Vicente et
120 al., 2014). DNP is characterised by the fact that it has rainy autumns and winters, and hot and
121 dry summers, all of which produce irregular inlets of water that determine the ungulates'
122 activity (Barasona et al., 2014a; Laguna et al., 2018). The Biological Reserve (BR) in the DNP,
123 which is located in its central region (see the red polygon in Figure 1), is the principal
124 management area (related to cattle production) that overlaps with our data, while the study area
125 considered herein was the Calibration Region (CR), in which sampled wild ungulate movement
126 patterns overlapped, using biologging and camera traps (blue polygon in Figures 1 and 2). CR
127 was employed as a study area (because all habitat conditions are within environmental domain
128 of the models, see Figure 1S), while BR and DNP were used to extrapolate the prediction
129 (because they have habitat conditions not necessarily within the domain of the model, as top
130 right and left pictures show in Figure 1S).

131

132 *2.2 Environmental predictors*

133 We selected the environmental predictors according to previous studies on wild ungulates'
134 habitat use in our study area (Barasona et al., 2014a; Laguna et al., 2018; Triguero-Ocaña et
135 al., 2020a): Euclidean distance (km) to the nearest artificial water hole (*dwat*); Euclidean
136 distance (km) to the nearest marsh–shrub ecotone (*dvera*); proportion of dense scrub dominated
137 by *Erica scoparia* and *Pistacia lentiscus* (*v1*); proportion of low-clear shrubland, composed
138 mainly of *Halimium halimifolium*, *Ulex minor* and *Ulex australis* (*v2*); proportion of

139 herbaceous grassland (v3); proportion of *Eucaliptus* sp. and *Pinus* sp. woodland (v4);
140 proportion of bare land, sandy dunes and beaches (v5), and proportion of watercourse
141 vegetation covered mainly by *Juncus* sp. patches (v6). For further descriptions of the layers,
142 see Barasona et al. (2014a). The original data were raster layers of 10x10 meters for land use
143 (v1-v6) and 100x100 meters for distances (*dvera* and *dwat*), but all were rescaled to 100x100
144 meter layers. These environmental predictors were estimated for each 100x100 meter grid that
145 covers all the non-flooded region of DNP.

146

147 *2.3 Resource selection functions and biologging data (RSF approach)*

148 We used data concerning seven red deer, six fallow deer and four wild boar monitored with
149 GPS-GSM collars (Microsensory System, Spain) from the second half of September to the first
150 half of December 2015, and from the second half of March to the first half of April 2016. These
151 animals were captured in the scrubland-marsh ecotone (“la vera”). The captures were carried
152 out by a specialised scientist (B and C experimentation categories) following the protocol
153 approved by the Animal Experiment Committee of Castilla-La Mancha University and by the
154 Spanish Ethics Committee (PR-2015-03-08; for further details, see Triguero-Ocaña et al.,
155 2020a). GPS-collars were set up to record one location every two hours, and had a mean
156 positioning error of 26 m (SD = 23.5 m). For each location, the collars also recorded the
157 individuals’ IDs, the date and the time (solar time). In order to obtain more similar and
158 equivalent data to that of the IDM, we restricted the locations to the period of animal activity.
159 Camera traps can detect animals only when they are active (Rowcliffe et al., 2014), while
160 biologging provides data from all hours of the day. The periods of activity of the species in the
161 study area (see Triguero-Ocaña et al., 2020b) were used as the basis on which to eliminate the

162 central hours of the day (from 9:00 to 19:00 h) in order to ensure that both data sources were
163 as comparable as possible.

164 Habitat use was assessed from biologging data by employing within-home-range resource-
165 selection functions (Manly et al., 2002). The environmental information for each location
166 considered in the RSF approach was assigned by using zonal statistics with the “extract”
167 function from the “raster” R package (Hijmans, 2020), in this case considering a buffer of a 26
168 m radius around each one (according to GPS positional error; see also Triguero-Ocaña et al.,
169 2020a). We compared the *used* versus *available* resources by using logistic regression mixed
170 models (Gillies et al., 2006), in which the individual was included as a random-effect factor,
171 and environmental characteristics were fixed factors. The use of resources was determined by
172 the locations of each individual, while the availability was sampled by randomly creating 10
173 times the number of locations (1:10 ratio of used to available points; Fieberg et al., 2021) within
174 each individual kernel home range 95% (Khr95). We assigned a weight of 5000 to the available
175 locations and a weight of 1 to the used locations (Fieberg et al., 2021). All these analyses were
176 performed using R v.3.6.2 (R-Core Team, 2019), with the “adehabitat” (Calenge, 2006), and
177 “glmmTMB” (Brooks et al., 2017) R packages.

178

179 *2.4 Imperfect detection models and camera trap data (IDM approach)*

180 Simultaneously to the biologging study (from the second half of September to the first half of
181 December 2015, and from the second half of March to the first half of April 2016), 38 and 27
182 cameras (LTL Acorn, LTL-5310 series) were placed in the study area in the 2015 and 2016
183 seasons, respectively, of which 4 and 1 cameras were discarded from the analyses owing to
184 operational problems (see Figure 2). The cameras were set on wooden stakes between 30 and
185 50 cm above the ground, were programmed to record 3 consecutive pictures per activation,

186 with less than 1 second between triggers and were active for 24 hours. Camera traps have been
187 established systematically with random origin, with a distance of 500 m between each of them
188 in 2015 and 1 km in 2016, and no bait was used in either season.

189 We employed imperfect detection hierarchical models to determine habitat use with the data
190 obtained from the camera traps (MacKenzie et al., 2002; Royle, 2004). The observational
191 process (detectability) was estimated by splitting the study period into five-day occasions
192 (sampling occasions) in order to avoid low detection probabilities (King et al., 2021),
193 considering each occasion as a visit and each camera trap as a sampling unit (site). We
194 additionally established a 10-minute window, such that detections more than 10 minutes apart
195 were considered as independent events (Tanwar et al., 2021). Detectability may vary according
196 to the site or survey characteristics, and we considered the occasion date (*time*) and the period
197 date (*year*) as observation covariates, and the type of dominant land use (*typeuse*; *i.e.* type of
198 land use that predominates at the sampling point) as a site covariate that could potentially affect
199 the detection process. The ecological process (relative abundance) relates only to site
200 characteristics, and we employed all the environmental predictors mentioned above as
201 covariates of site. The environmental information concerning each of these variables was
202 assigned to each camera trap using zonal statistics with the “extract” function from the “raster”
203 R package (Hijmans, 2020). With regard to our study species (red deer, fallow deer and wild
204 boar), we determined intensity of use by comparing the differences in the animals’ relative
205 abundance around each camera trap (assuming that the fitness of a species is correlated with
206 population density; Boyce et al., 2016), taking into account the environmental characteristics
207 of each site by using counts of detections and single-season N-mixture models (Royle, 2004).
208 As the focus was on spatial variation in habitat use, we used single-season models, while *year*
209 was also included in the ecological process as a fixed factor in order to control for differences
210 in intensity of use depending on the season. Another possible approach would have been the

211 use of site-occupancy models (MacKenzie et al., 2002), which employ detection/non-detection
212 histories (0/1) as input data. However, given the small size of our sampling area and the high
213 average occupancy for two species (high percentage of study area occupied, see percentage of
214 cameras with detections in Table 1S), we decided to use detection counts within an N-mixture
215 modelling framework so as to incorporate as much as heterogeneity in habitat use for each
216 species. Since it was not possible to meet the strict set of assumptions required by N-mixture
217 models in order to obtain total abundance estimations (e.g. population sampled in closed units),
218 we interpreted our model predictions as relative abundance or simply as intensity of habitat use
219 (Searle et al. 2020). All analyses were performed using R v. 3.6.2 (R-Core Team, 2019), with
220 the “unmarked” package (Fiske & Chandler, 2011).

221

222 *2.5 Model selection and predictions*

223 The best model for each approach was selected by following a backward stepwise selection
224 procedure based on Akaike’s information criteria (AIC). This procedure consists of starting
225 with the full model (all predictor variables included), and in each step, removing the variable
226 that most decreases the AIC score when removed. The stepwise procedure is stopped when it
227 is not possible to improve the model by removing additional predictors. We maintained the
228 model with lowest AIC and all the models with a similar fit (AIC difference lower than 2 units;
229 Burnham & Anderson, 2002). In those cases in which more than one model was available, we
230 create an average model based in these models, applying a weight to each model based on its
231 AIC by using the “model.avg” function of “MuMIn” package (Burnham & Anderson, 2002).

232 Once the best model had been selected (one per species and approach), it was projected at a
233 resolution of 100x100 meter in order to predict species intensity of habitat use in the CR by
234 using the “predict” function from the “raster” R package (Hijmans, 2020). We comparatively

235 assessed concordance between spatial patterns from each approach used for the CR, and also
236 predicted the BR and DNP level so as to explore the consistence between approaches when the
237 models were extrapolated (outside the domain of the model, see *dvera* and *dwat* in Figure 1S).
238 This was done by carrying out a reclassification in quartiles (0-25%, 25-50%, 50-75% and 75-
239 100%) beforehand in order to avoid problems resulting from a different scale in the predictions,
240 and led to the attainment of a common intensity of habitat use level category (levels from lowest
241 to highest adequacy of the environment for the species). The agreement between the predictions
242 was estimated by using a weighted Cohen's kappa coefficient (Cohen, 1960). The weighted
243 kappa is a modification of Cohen's kappa that considers the closeness of agreement between
244 categories when there are more than two, penalising the disagreement with greater force when
245 the difference between categories is greater. The index ranges from -1 (complete disagreement)
246 to 1 (complete agreement), and the value 0 indicates a concordance similar to that expected by
247 chance. In our case, we employed a matrix of weights established as 0 on the diagonal and the
248 distance from the diagonal squared outside of the diagonal (default conditions; Reville, 2015).

249

250 3. RESULTS

251 Both approaches, i.e. RSF and IDM, were compared in terms of the explanatory variables
252 selected and the spatial patterns predicted. In the case of red deer, the main variables
253 highlighted by the RSF approach were related to wet enclosed areas (by considering estimates
254 p-value and z-value weights; see the model in Table 1). With regard to the IDM approach, the
255 main variable was related to wet areas in the relative abundance process, and *year* and *time* in
256 the detection process (Table 1). The agreement between the predictions generated by the two
257 approaches (Figure 3) was, according to Cohen's weighted kappa coefficient, 0.225 (with a
258 confidence interval [CI] of 95% from 0.181 to 0.270) at the CR level, 0.221 (CI95% from 0.210
259 to 0.235) at the BR level, and 0.112 (CI95% from 0.101 to 0.123) at the DNP level (Figure 3).

260 In the case of wild boar, the main variable highlighted in the RSF approach was related to wet,
261 dry and enclosed areas (Table 1). With regard to the IDM approach, the main variables were
262 enclosed, dry and wet areas in the relative abundance process, and *year* in the detection process
263 (Table 1). The agreement between the predictions generated by the two approaches for wild
264 boar (Figure 3) was, according to Cohen's weighted kappa coefficient, 0.260 (CI95% from
265 0.210 to 0.311) at the CR level, 0.490 (CI95% from 0.470 to 0.510) at the BR level, and 0.580
266 (CI95% from 0.570 to 0.590) at the DNP level (Figure 3).

267 Finally, in the case of fallow deer, the main variables highlighted in the RSF approach were
268 related to wet and enclosed areas (Table 1). With regard to the IDM approach, the main
269 variables were related to enclosed and wet areas in the relative abundance process, and *year* in
270 the detection process (Table 1). In this case, the agreement between predictions generated by
271 the two approaches (Figure 3) was, according to Cohen's weighted kappa coefficient, 0.150
272 (CI95% from 0.113 to 0.190) at the CR level, 0.360 (CI95% from 0.330 to 0.390) at the BR
273 level, and 0.550 (CI95% from 0.540 to 0.550) at the DNP level (Figure 3).

274

275 **4. DISCUSSION**

276 Several comparative studies of different methodologies with which to study animal habitat use
277 have been carried out (e.g. Mulero-Pázmány et al., 2015). Modern analytical approaches whose
278 purpose is to take into account imperfect detection (such as site-occupancy or N-mixture
279 models) have become popular in species occupancy and abundance modelling in recent years,
280 and have consequently become complementary approaches to classical approaches already
281 established in various research topics (e.g. Duquette et al., 2014; Meyer et al., 2020), one of
282 which is the study of the habitat use (Coleman et al., 2014). The results obtained in this study
283 suggest that RSF and IDM can produce partly comparable interpretations concerning intensity

284 of habitat use, but that there are notable differences between them which vary according to
285 species. The lack of support for equivalence between IDM and RSF approaches in our study
286 support our hypothesis, but more studies using different populations, species, scales,
287 contrasting environments and particularly longer periods of data collection should be carried
288 out in order to verify our results. Moreover, these discrepancies could indicate that each
289 approach captures different information on populations of the same species (Bassing et al.,
290 2022), and a combination of both approaches could overcome the limitations of each one and
291 improve the descriptions of wildlife habitat selection.

292 Our first objective was to discover whether the IDM approach was able to detect the main
293 environmental gradients by determining intensity of habitat use in the same way that the RSF
294 approach does. The tendency of both approaches to agree or not depends on the species. The
295 common explanatory variables in the red deer models obtained for both approaches were those
296 related to proximity to wet environments (*dvera* and *dwat*; see Table 1), but the RSF approach
297 highlighted a preference for shrubland landscapes (*v2*, given that it shows a negative trend of
298 all land uses, except *v2* that is missing), in addition to avoiding forest areas (*v4*; Table 1), which
299 was what produced the difference between both approaches. All these tendencies are consistent
300 with previous studies carried out under Mediterranean climate conditions (e.g. Alves et al.,
301 2014; Barasona et al., 2014a; Braza & Álvarez, 1987). The wild boar attained a negative
302 relationship with shrubland (*v1* and *v2*) and drier areas (*v5*) for both approaches (Table 1), and
303 this coincides with previous studies, which have shown that the wild boar avoids of shrubland
304 during its activity period (Acevedo et al., 2006, 2014). Additionally, the RSF approach
305 highlighted a clear tendency towards wet (*dwat* and *v6*) and herbaceous areas (*v3*; Table 1),
306 and this dependence on water and herbaceous points in the driest season has also been shown
307 in previous studies (Abaigar et al., 1994; Barasona et al., 2014b). Nevertheless, although RSF
308 approach selected more environmental factors, both indicated the same trend, highlighting the

309 water sources as a key factor in southern Spain. With regard to the fallow deer, both approaches
310 coincide, showing a tendency to avoid more enclosed areas (*v1* and *v2*) and a strong preference
311 for wet environments (*dwat* and *dvera*; Table 1), similar to the results obtained in previous
312 studies (Braza & Álvarez, 1987). However, the RSF approach also included an avoidance of
313 forest areas (*v4*, in IDM it was not statistically significant; Table 1), as has occurred in previous
314 studies (Barasona et al., 2014a; Braza & Álvarez, 1987).

315 The RSF models were, in general, more complex for all the species (i.e. included a larger
316 number of statistically significant predictors). This difference between approaches could be
317 principally owing to the quantity and quality of the different sources of data: GPS collars record
318 near continuous spatial data, no matter where the animal is moving, but at an individual level
319 (Hebblewhite & Haydon, 2010), whereas camera traps can obtain near continuous temporal
320 detections of many individuals at a population level, but are limited to specific survey points
321 (Burton et al., 2015; Iannarilli et al., 2021; O'Connell et al., 2011). Camera traps monitor finite
322 space and locations, thus limiting the extent and resolution of inference and, therefore, the
323 power to estimate the effects of multiple predictors at once (Bailey et al., 2007; Phillips et al.,
324 2019; Wakefield et al., 2011; Watanuki et al., 2016). When using camera traps it is
325 consequently necessary to employ a large number of sampling points in order to obtain the
326 quantity of variation required to obtain intensity of habitat use precise predictions from
327 complex models and avoid bias in the sampling process (Burton et al., 2015; Hofmeester et al.,
328 2019; Iannarilli et al., 2021; Tanwar et al., 2021).

329 Our second objective was to explore the consistency of the predicted patterns of intensity of
330 habitat use in each approach. In this respect, we obtained differences in consistence among the
331 species at the three levels: CR, BR and DNP. These types of discrepancies in predictions have
332 already been seen in previous studies (Bassing et al., 2022; Phillips et al., 2019). Concretely,
333 agreement was obtained for all the species in the study area (CR level; see Figure 3). The best

334 concordance was observed for wild boar, followed by fallow deer and red deer (Figure 3),
335 which may be related to the similarity of the explanatory factors in the RSF and IDM
336 approaches for each species (Table 1). Nevertheless, prediction agreement followed different
337 trends when extrapolated (BR and DNP level), depending on the species, and agreement
338 decreased when comparisons were made on larger scales (CR > BR > DNP; see the visual
339 pattern and Kappa coefficient in Figure 3) for red deer, while agreement increased with scale
340 (DNR > BR > CR; Figure 3) for wild boar and fallow deer. One possible explanation for this
341 discrepancy could be related to the models' capacity to capture the complete environmental
342 gradient of the species in the sampled area. When the more relevant gradients for the species
343 are not included in the model, imprecise predictions could be produced in the study area, and
344 higher discrepancies in new (extrapolated) territories (Elith & Leathwick, 2009; see differences
345 in covariate gradients between methods and/or levels of prediction in Figure 1S, as differences
346 in quantity of data of typeuse $v1$ and $v2$ between approaches). According to this hypothesis,
347 the models for red deer produce under-representative predictions (in one or both approaches),
348 and the disagreement between them increases when they are extrapolated. In the case of wild
349 boar and fallow deer, both predictions were able to capture the environmental characteristics
350 of the preferred areas and, therefore, provided good descriptions of the general patterns on large
351 spatial scales (increasing the agreement to these scales).

352 When the intensity of habitat use patterns obtained were compared with those shown in
353 previously published studies, IDM approach for red deer was more concordant (Barasona et
354 al., 2014a). In the case of wild boar and fallow deer, both approaches were similar to those
355 shown in previous works (Barasona et al., 2014a, 2014b). One reason for the discordance
356 between the red deer RSF model and those shown in previous works may be the short data-
357 collection period employed and/or a scarce number of individuals monitored, which could have
358 produced bias (caused by a lack of time and/or individuals sampling data). As a general

359 recommendation, employing longer periods in both approaches, along with establishing more
360 sampling points in the case of IDM and more individual in the case of RSF, could lead to more
361 robust predictions, since it would be possible to provide a good characterisation of all the
362 habitats and preferences (Bassing et al., 2022; Phillips et al., 2019).

363 Our study showed that each approach differed as regards the main variables that influenced
364 intensity of habitat use, but that all the selected variables are, to some extent, refuted by
365 previous research. This may indicate that both methodologies can correctly determine habitat
366 use, but that each of them identifies different features (Bassing et al., 2022). This is something
367 that could be expected if we look at the key peculiarities of each approach, where RSF collects
368 data at the individual level and analyzes habitat use against availability within each animal's
369 home range, while camera trapping works at the population level in specific sites, comparing
370 the relative abundance between the different sampled points. Therefore, the RSF approach is
371 relating the predictor variables to the relative probability of selection within home range, while
372 the IDM approach is relating the predictor variables to relative abundance differences between
373 sampled sites. One reason of discrepancies based on these key peculiarities is the multi-scale
374 interaction of the species with the environment (McGarigal et al., 2016), signifying that each
375 approach detects some scales better than others. This may be owing to these key peculiarities
376 of each approach (concretely individual-specific data in RSF vs. site-specific data in IDM).
377 The RSF approach may, therefore, focus more on the within home range habitat selection (3rd
378 order of Johnson's four levels of habitat selection), while the IDM approach may focus on the
379 home range habitat selection (2nd order of Johnson's levels), bearing in mind that the variables
380 that affect each level are not necessarily the same (Bassing et al., 2022; Boyce, 2006; Cushman
381 & McGarigal, 2004). Another reason could be that each approach obtains a different range of
382 values for the predictors (see differences between approaches in ranges as *dvera* or *v6*; Figure
383 S1), sampling different components of the same population's habitat use (Bassing et al., 2022).

384 In other words, one approach obtains more variability from some predictor variables, and the
385 other obtains more variability from others, and the set of predictors with greater variability may
386 have more weight in each model. This may be related to the limitations of each model, where
387 the IDM only obtains data on the predictors in a finite number of sampling points, the RSF
388 obtains them from a finite number of home range of monitored animals. According to the
389 results obtained in the present work, the use of biologging as a classic tool in habitat use studies,
390 and the increase in the use of camera trapping in the last decades as a novel tool (Rovero &
391 Zimmermann, 2016), show that both methods are complementary, and that approach greatly
392 depends on the objective of the study. The complementary information contained in each kind
393 of data therefore indicates that data integration is a promising tool with which to obtain the
394 more informative and precise models of habitat selection required in order to support decision-
395 making in wildlife management and conservation (Apollonio et al., 2017; Fletcher et al., 2019;
396 Isaac et al., 2020; Miller et al., 2019).

397

398 **5. CONCLUSIONS**

399 The two approaches tested, i.e. RSF and IDM, were not equivalent as regards identifying the
400 main environmental gradients that explain the intensity of habitat use of the species studied:
401 red deer, wild boar and fallow deer. The spatial patterns of habitat use have a greater or a lower
402 level of agreement depending on the species studied. The spatial patterns maintained (and
403 sometimes increased) the agreement between approaches beyond the study area (Biological
404 Reserve and Doñana National Park) as long as the predictions were representative of the
405 complete environmental gradient. Both approaches determined intensity of habitat use patterns
406 well, but identified different features of it, probably because IDM relates environmental
407 features to differences in relative abundance to a population level, while RSF relates

408 environmental features to the relative probability of use at individual level. If the need arises
409 to choose between both methodologies, it is, therefore, necessary to consider which best fits
410 the proposed objective, or whether it is possible to combine both, thus resulting in the
411 attainment of more informative and more precise habitat selection models. Future studies
412 should consider repeating this comparison of approaches with longer periods of data collection
413 and on more patchy landscapes in order to obtain a more robust conclusion.

414

415 **CRedit authorship contribution statement**

416 **David Ferrer-Ferrando:** Conceptualization, Methodology, Validation, Formal analysis,
417 Investigation, Writing-Original Draft, Writing-Review & Editing, Visualization. **Javier**
418 **Fernández-López:** Conceptualization, Methodology, Validation, Formal analysis,
419 Investigation, Writing-Review & Editing, Visualization, Supervision. **Roxana Triguero-**
420 **Ocaña:** Investigation, Resources, Data Curation, Writing-Review & Editing. **Pablo Palencia:**
421 Investigation, Resources, Data Curation, Writing-Review & Editing. **Joaquín Vicente:**
422 Conceptualization, Investigation, Resources, Data Curation, Writing-Review & Editing,
423 Funding acquisition. **Pelayo Acevedo:** Conceptualization, Methodology, Validation, Formal
424 analysis, Investigation, Resources, Data Curation, Writing-Review & Editing, Visualization,
425 Supervision, Project administration, Funding acquisition.

426

427 **Acknowledgements**

428 We would like to thank all those who have participated in the capture and collaring of wild
429 ungulates, and in the setting of camera traps.

430

431 **Data availability**

432 Data employed for N-mixture models and resource selection functions are available in Zenodo
433 at <https://doi.org/10.5281/zenodo.7766936>. Code employed in the analysis is available in
434 Zenodo at <https://doi.org/10.5281/zenodo.7766936>. The following data supporting this
435 research are sensitive and not available publicly: coordinates of telemetry relocations from
436 GPS-collared animals and camera trap locations.

437

438 **Funding**

439 DFF received a Start to Research grant for Master's degree students, financed by the
440 collaboration agreement between the University of Castilla-La Mancha and the Banco
441 Santander (2019-UNIVERS-9556), which allowed him to commence this study, and he also
442 obtained support from the UCLM through a predoctoral scholarship (2020-PREDUCLM-
443 16022), which allowed him to continue with this research. JFL was funded by the Margarita
444 Salas grant from the European Union – NextGenerationEU through the Complutense
445 University of Madrid. PP received support from University of Castilla-La Mancha through a
446 Margarita Salas contract (2022-NACIONAL-110053). Our research group is partly supported
447 by Applied Research Projects (2022-GRIN-34227) funded by UCLM-FEDER

448

449 **Declaration of competing interest**

450 The authors declare that they have no known competing financial interests or personal
451 relationships that could have appeared to influence the work reported in this paper.

452

453 **Bibliography**

454 Abaigar, T., Del Barrio, G., & Vericad, J. R. 1994. Habitat preference of wild boar (*Sus scrofa*
455 L., 1758) in a Mediterranean environment. Indirect evaluation by signs. *Mammalia*, 58(2),
456 201-210.

457 Acevedo, P., Escudero, M. A., Muñoz, R., & Gortázar, C. 2006. Factors affecting wild boar
458 abundance across an environmental gradient in Spain. *Acta Theriologica*, 51(3), 327-336.

459 Acevedo, P., Quirós-Fernández, F., Casal, J., & Vicente, J. 2014. Spatial distribution of wild
460 boar population abundance: Basic information for spatial epidemiology and wildlife
461 management. *Ecological Indicators*, 36, 594-600.

462 Alves, J., da Silva, A. A., Soares, A. M., & Fonseca, C. 2014. Spatial and temporal habitat use
463 and selection by red deer: The use of direct and indirect methods. *Mammalian*
464 *Biology*, 79(5), 338-348.

465 Apollonio, M., Belkin, V. V., Borkowski, J., Borodin, O. I., Borowik, T., Cagnacci, F., ... &
466 Gaillard, J. M. 2017. Challenges and science-based implications for modern management
467 and conservation of European ungulate populations. *Mammal research*, 62(3), 209-217.

468 Bailey, L. L., Hines, J. E., Nichols, J. D., & MacKenzie, D. I. 2007. Sampling design trade-offs
469 in occupancy studies with imperfect detection: examples and
470 software. *Ecological Applications*, 17(1), 281-290.

471 Barasona, J. A., Mulero-Pázmány, M., Acevedo, P., Negro, J. J., Torres, M. J., Gortázar, C., &
472 Vicente, J. 2014a. Unmanned aircraft systems for studying spatial abundance of ungulates:
473 Relevance to spatial epidemiology. *PLoS ONE*, 9(12), 1-17.

474 Barasona, J. A., Latham, M. C., Acevedo, P., Armenteros, J. A., Latham, A. D. M., Gortazar,
475 C., ... & Vicente, J. 2014b. Spatiotemporal interactions between wild boar and cattle:
476 implications for cross-species disease transmission. *Veterinary research*, 45(1), 122.

477 Bassing, S. B., Devivo, M., Ganz, T. R., Kertson, B. N., Prugh, L. R., Roussin, T., ... & Gardner,
478 B. 2022. Are we telling the same story? Comparing inferences made from camera trap
479 and telemetry data for wildlife monitoring. *Ecological Applications*, e2745.

480 Begon, M., Townsend, C. R., & Harper, J. L. 2006. *Ecology: from individuals to*
481 *ecosystems* (No. Sirsi) i9781405111171).

482 Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions*, 12(3),
483 269-276.

484 Boyce, M. S., Johnson, C. J., Merrill, E. H., Nielsen, S. E., Solberg, E. J., & Van Moorter, B.
485 2016. Can habitat selection predict abundance?. *Journal of Animal Ecology*, 85(1), 11-20.

486 Braza, F., & Álvarez, F. 1987. Habitat use by red deer and fallow deer in Doñana National
487 Park. *Miscel·lània Zoològica*, 363-367.

488 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A.,
489 ... & Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for
490 zero-inflated generalized linear mixed modeling. *The R journal*, 9(2), 378-400.

491 Burnham, K. P., & Anderson, D. R. 2002. Model selection and multimodel inference. *A*
492 *practical information-theoretic approach, 2nd ed. Springer, New York, 2.*

493 Burton, A.C., Neilson, E.W., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E.M.,
494 & Boutin, S. 2015. REVIEW: Wildlife camera trapping: a review and recommendations
495 for linking surveys to ecological processes. *Journal of Applied Ecology*, 52, 675-685.

496 Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space
497 and habitat use by animals. *Ecological modelling*, 197(3-4), 516-519.

498 Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and
499 productivity. *BioScience*, 31(2), 107-113.

500 Cohen, J. A. 1960. Educational and psychological measurement. *Coefficient of agreement for*
501 *nominal scales*, 20, 37-46.

502 Coleman, L. S., Ford, W. M., Dobony, C. A., & Britzke, E. R. 2014. Comparison of radio-
503 telemetric home-range analysis and acoustic detection for little brown bat habitat
504 evaluation. *Northeastern Naturalist*, 21(3), 431-445.

505 Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., &
506 Butler, P. J. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in ecology &*
507 *evolution*, 19(6), 334-343.

508 Cushman, S. A., & McGarigal, K. 2004. Patterns in the species–environment relationship
509 depend on both scale and choice of response variables. *Oikos*, 105(1), 117-124.

510 Delisle, Z. J., Flaherty, E. A., Nobbe, M. R., Wzientek, C. M., & Swihart, R. K. 2021. Next-
511 generation camera trapping: systematic review of historic trends suggests keys to
512 expanded research applications in ecology and conservation. *Frontiers in Ecology and*
513 *Evolution*, 9, 617996.

514 Duquette, J. F., Belant, J. L., Svoboda, N. J., Beyer, D. E., &
515 Albright, C. A. 2014. Comparison of occupancy modeling and radiotelemetry to estimate
516 ungulate population dynamics. *Population Ecology*, 56(3), 481-492.

517 Elith, J., & Leathwick, J. R. 2009. Species distribution models: ecological explanation and
518 prediction across space and time. *Annual Review of Ecology, Evolution and*
Systematics, 40(1), 677-697.

519 Fieberg, J., Signer, J., Smith, B., & Avgar, T. 2021. A ‘How to’ guide for interpreting
520 parameters in habitat-selection analyses. *Journal of Animal Ecology*, 90(5), 1027-1043.

521 Fiske, I., & Chandler, R. 2011. Unmarked: an R package for fitting hierarchical models of
522 wildlife occurrence and abundance. *Journal of statistical software*, 43(10), 1-23.

523 Fletcher Jr, R. J., Hefley, T. J., Robertson, E. P., Zuckerberg, B., McCleery, R. A., & Dorazio,
524 R. M. 2019. A practical guide for combining data to model species
525 distributions. *Ecology*, 100(6), e02710.

526 Gilbert, N. A., Clare, J. D., Stenglein, J. L., & Zuckerberg, B. 2021. Abundance estimation of
527 unmarked animals based on camera-trap data. *Conservation Biology*, 35(1), 88-100.

528 Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L.,
529 ... & Jerde, C. L. 2006. Application of random effects to the study of resource selection
530 by animals. *Journal of Animal Ecology*, 75(4), 887-898.

531 Goulart, F. V. B., Cáceres, N. C., Graipel, M. E., Tortato, M. A., Ghizoni Jr, I. R., & Oliveira-
532 Santos, L. G. R. 2009. Habitat selection by large mammals in a southern Brazilian Atlantic
533 Forest. *Mammalian Biology*, 74(3), 182-190.

534 Gould, M. J., Gould, W. R., Cain, J. W., & Roemer, G. W. 2019. Validating the performance
535 of occupancy models for estimating habitat use and predicting the distribution of highly-
536 mobile species: A case study using the American black bear. *Biological Conservation*,
537 234(March), 28-36.

538 Hebblewhite, M., & Haydon, D. T. 2010. Distinguishing technology from biology: a critical
539 review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the*
540 *Royal Society B: Biological Sciences*, 365(1550), 2303-2312.

541 Hijmans, R. J. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-
542 6. <https://CRAN.R-project.org/package=raster>

543 Hofmeester, T. R., Cromsigt, J. P., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. 2019.
544 Framing pictures: A conceptual framework to identify and correct for biases in detection
545 probability of camera traps enabling multi-species comparison. *Ecology and*

546 *Evolution*, 9(4), 2320-2336.

547 Iannarilli, F., Erb, J., Arnold, T. W., & Fieberg, J. R. 2021. Evaluating species-specific
548 responses to camera-trap survey designs. *Wildlife Biology*, 2021(1), 1-12.

549 Isaac, N. J., Jarzyna, M. A., Keil, P., Dambly, L. I., Boersch-Supan, P. H., Browning, E., ... &
550 O'Hara, R. B. 2020. Data integration for large-scale models of species
551 distributions. *Trends in ecology & evolution*, 35(1), 56-67.

552 Jiménez, J., Higuero, R., Charre-Medellin, J. F., Acevedo, P. 2017. Spatial mark-resight models
553 to estimate feral pig population density. *Hystrix, the Italian Journal of Mammalogy*, 28(2),
554 208-213. Kelly, M. J., & Holub, E. L. 2008. Camera trapping of carnivores: trap success
555 among camera types and across species, and habitat selection by species, on salt pond
556 mountain, Giles County, Virginia. *Northeastern Naturalist*, 15(2), 249–262.

557 King, T. W., Vynne, C., Miller, D., Fisher, S., Fitkin, S., Rohrer, J., ... & Thornton, D. H. 2021.
558 The influence of spatial and temporal scale on the relative importance of biotic vs. abiotic
559 factors for species distributions. *Diversity and Distributions*, 27(2), 327-343.

560 Laguna, E., Barasona, J. A., Triguero-Ocaña, R., Mulero-Pázmány, M., Negro, J. J., Vicente,
561 J., & Acevedo, P. 2018. The relevance of host overcrowding in wildlife epidemiology: A
562 new spatially explicit aggregation index. *Ecological Indicators*, 84, 695-700.

563 Levins, R. 1968. *Evolution in changing environments: some theoretical explorations* (No. 2).
564 Princeton University Press.

565 MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J.A., & Langtimm, C. A.
566 2002. Estimating site occupancy rates when detection probabilities are less than
567 one. *Ecology*, 83(8), 2248-2255.

568 MacKenzie, D. I., & Royle, J. A. 2005. Designing occupancy studies: general advice and

569 allocating survey effort. *Journal of Applied Ecology*, 42(6), 1105-1114.

570 Manly, B. F. J., McDonald L. L., Thomas D. L., McDonald T. L., & Erickson W. P. 2002.
571 *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*, 2nd ed.
572 Boston, MA: Kluwer Academic Press.

573 McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. 2016. Multi-scale
574 habitat selection modeling: a review and outlook. *Landscape ecology*, 31(6), 1161-1175.

575 Meyer, N. F. V., Moreno, R., Reyna-Hurtado, R., Signer, J., & Balkenhol, N. 2020. Towards
576 the restoration of the Mesoamerican Biological Corridor for large mammals in Panama:
577 Comparing multi-species occupancy to movement models. *Movement Ecology*, 8(1), 1-
578 14.

579 Miller, C. S., Hebblewhite, M., Goodrich, J. M., & Miquelle, D. G. 2010. Review of research
580 methodologies for tigers : Telemetry. *Integrative Zoology*, 378-389.

581 Miller, D. A., Pacifici, K., Sanderlin, J. S., & Reich, B. J. 2019. The recent past and promising
582 future for data integration methods to estimate species' distributions. *Methods in Ecology
583 and Evolution*, 10(1), 22-37.

584 Mulero-Pázmány, M., Barasona, J. Á., Acevedo, P., Vicente, J., & Negro, J. J. 2015. Unmanned
585 Aircraft Systems complement biologging in spatial ecology studies. *Ecology and
586 Evolution*, 5(21), 4808-4818.

587 O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. *Camera traps in animal ecology:
588 methods and analyses*. A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. New
589 York, New York: Springer. Orians, G. H. 1980. Habitat selection: General theory and
590 applications to human behavior. *The evolution of human social behavior*.

591 Phillips, E. M., Horne, J. K., Zamon, J. E., Felis, J. J., & Adams, J. 2019. Does perspective

592 matter? A case study comparing Eulerian and Lagrangian estimates of common murre
593 (*Uria aalge*) distributions. *Ecology and Evolution*, 9(8), 4805-4819.

594 R Core Team 2019. R: A language and environment for statistical computing. R Foundation
595 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

596 Recio, M. R., Mathieu, R., Maloney, R., & Seddon, P. J. 2011. Cost comparison between GPS-
597 and VHF-based telemetry: case study of feral cats *Felis catus* in New Zealand. *New*
598 *Zealand Journal of Ecology*, 114-117.

599 Revelle, W. 2015. Find Cohen's kappa and weighted kappa coefficients for correlation of two
600 raters. R: Find Cohen's kappa and weighted kappa coefficients for... (personality-
601 project.org)

602 Rovero, F., Tobler, M., & Sanderson, J. 2010. Camera trapping for inventorying terrestrial
603 vertebrates. In: Eymann J., Degreef J., Häuser C., Monje J.C., Samyn Y., VandenSpiegel
604 D. (Eds.). Manual on field recording techniques and protocols for all taxa biodiversity
605 inventories and monitoring. *The Belgian National Focal Point to the Global Taxonomy*
606 *Initiative*, 8, 100-128.

607 Rovero, F., & Zimmermann, F. 2016. Camera Trapping for Wildlife Research. Exeter. *Pelagic*
608 *Publishing*, UK.

609 Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. 2014. Quantifying
610 levels of animal activity using camera trap data. *Methods in ecology and evolution*, 5(11),
611 1170-1179.

612 Royle, J. A. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated
613 Counts. *Biometrics*, 60(1), 108-115.

614 Schofield, G., Bishop, C. M., Katselidis, K. A., Dimopoulos P., Pantis, J. D., and Hays, G. C.

615 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment.
616 *Journal of Animal Ecology* 78:14–21.

617 Searle, C. E., Bauer, D. T., Kesch, M. K., Hunt, J. E., Mandisodza-Chikerema, R., Flyman, M.
618 V., ... & Loveridge, A. J. 2020. Drivers of leopard (*Panthera pardus*) habitat use and
619 relative abundance in Africa's largest transfrontier conservation area. *Biological*
620 *Conservation*, 248, 108649.

621 Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., ... & Brodie,
622 J. 2017. Scaling-up camera traps: Monitoring the planet's biodiversity with networks of
623 remote sensors. *Frontiers in Ecology and the Environment*, 15(1), 26-34.

624 Tanwar, K. S., Sadhu, A., & Jhala, Y. V. 2021. Camera trap placement for evaluating species
625 richness, abundance, and activity. *Scientificreports*, 11(1), 1-11.

626 Triguero-Ocaña, R., Martínez-López, B., Vicente, J., Barasona, J. A., Martínez-Guijosa, J., &
627 Acevedo, P. 2020a. Dynamic network of interactions in the wildlife-livestock interface in
628 mediterraneanspain: An epidemiological point of view. *Pathogens*, 9(2).

629 Triguero-Ocaña, R., Vicente, J., Palencia, P., Laguna, E., & Acevedo, P. 2020b. Quantifying
630 wildlife-livestock interactions and their spatio-temporal patterns: Is regular grid camera
631 trapping a suitable approach?. *Ecological Indicators*, 117, 106565.

632 Vicente, J., Soriguer, R., Gortázar, C., Carro, F., Acevedo, P., Barasona, J. A., ... & Negro, J.
633 J. 2014. Bases técnicas para una extracción sostenible de ungulados del Parque Nacional
634 de Doñana. *Unpublished results*.

635 Wakefield, E. D., Phillips, R. A., Trathan, P. N., Arata, J., Gales, R., Huin, N., ...
636 &Matthiopoulos, J. 2011. Habitat preference, accessibility, and competition limit the
637 global distribution of breeding Black-browed Albatrosses. *Ecological*

638 *Monographs*, 81(1), 141-167.

639 Watanuki, Y., Suryan, R. M., Sasaki, H., Yamamoto, T., Hazen, E. L., Renner, M., ...
640 &Sydeman, W. J. 2016. *Spatial ecology of marine top predators in the North Pacific:*
641 *Tools for integrating across datasets and identifying high use areas.* North Pacific Marine
642 Science Organization (PICES).

643 Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., &Yovovich, V. 2015. The
644 golden age of bio-logging: how animal-borne sensors are advancing the frontiers of
645 ecology. *Ecology*, 96(7), 1741-1753.

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659 **Figure captions**

660 Figure 1. Study area location. The Biological Reserve (principal management area that overlaps
661 with our data; red continuous line) and the Calibration Region (our study area; blue
662 discontinuous line) are located in Doñana National Park (grey area).

663 Figure 2. Calibration Region (blue line) and Biological Reserve (red line), showing the home
664 range (kernel 95%) of collared individuals by species (A) and the grid of camera traps by
665 sampling period (B).

666 Figure 3. Predicted patterns of habitat intensity of use for wild ungulates in the Calibration
667 Region (blue line). The Biological Reserve (red line) and Doñana National Park have been
668 delimited in order to extrapolate predictions. The approaches were resource selection functions
669 obtained from biologging derived data (RSF approach) and imperfect detection models
670 obtained from camera trap data (IDM approach). Maps represent IDM (A) and RSF approach
671 (B) for red deer; IDM (C) and RSF approach (D) for wild boar; and IDM (E) and RSF approach
672 (F) for fallow deer. Habitat intensity of use patterns were divided into four levels (quantiles) in
673 order to assess the agreement between the predictions produced by the approaches with Cohen's
674 weighted kappa coefficient at three different levels of extension, with their respective 95%
675 confidence interval values in brackets: Calibration Region (study area, in blue), Biological
676 Reserve (in red) and Doñana National Park (in black).

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