Uniform performance of mammal detection methods under contrasting environmental conditions in Mediterranean landscapes

BRUNO D. SUÁREZ-TANGIL and ALEJANDRO RODRÍGUEZ

Department of Conservation Biology, Estación Biológica de Doñana – CSIC, Américo Vespucio 26, Sevilla 41092 Spain

Citation: Suárez-Tangil, B. D., and A. Rodríguez. 2021. Uniform performance of mammal detection methods under contrasting environmental conditions in Mediterranean landscapes. Ecosphere 12(3):e03349. 10.1002/ecs2.3349

Abstract. Monitoring local occupancy and the regional distribution of wild mammals is essential to guide species management and set conservation priorities. However, variables such as weather, substrate hardness, or habitat characteristics may indirectly affect the performance of the methods employed for monitoring mammal occurrence. Little information exists about the influence of spatio-temporal factors on the performance of survey methods and its implications for mammal monitoring. Using data from a heterogeneous region in the Guadiamar River basin, SW Spain, which encompass forest, agricultural, and mosaic landscapes, we (1) explore whether four widely used detection methods, namely camera traps, scent stations, track surveys, and scat surveys, differ in efficiency; (2) test the hypothesis that spatio-temporal factors do not affect method efficiency; and (3) examine the effect of landscape on the replication effort needed to detect target species. After controlling for variation in mammal occurrence across space and over time, the interaction between spatio-temporal factors and detection methods was not significant. Likewise, we found a negligible influence of landscape type on the replication effort needed to detect species actually present. When compared to camera traps, scent stations, and scat surveys, track surveys were the most efficient and fastest methodology for surveying mammals in our study landscapes. Monitoring programs of mammal occurrence are often applied to broad and heterogeneous regions and/or during extended periods. Therefore, survey methods should describe not only spatio-temporal variation in mammal abundance or activity but also maintain high detection efficiency in a variety of environmental conditions. The detection efficiency of each survey method changed little regardless of considerable environmental variation, making more reliable the marked differences between methods in their ability to detect target species. We recommend accounting for the effect of spatio-temporal factors as potential sources of variation in order to test whether our results can be generalized and to increase the quality of large-scale monitoring of mammal occurrence.

Key words: camera traps; efficiency; environmental conditions; large-scale surveys; mammal monitoring; Mediterranean; method performance; replication effort; scat surveys; scent stations; spatio-temporal factors; track surveys.

Received 1 April 2020; revised 12 June 2020; accepted 2 October 2020; final version received 12 November 2020. Corresponding Editor: Rebecca J. Rowe.

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INTRODUCTION

Monitoring local occupancy and the regional distribution of wild mammals is essential to guide species management (Sarre et al. 2012) and set conservation priorities (Kong et al. 2017). Accurate knowledge of species occurrence (Thorn et al. 2011, McCarthy et al. 2015), together
with methodological approaches that predict species response to fast drivers of global change (Araújo et al. 2019, La Marca et al. 2019), is fundamental to identify conservation priority areas (Bonnet-Lebrun et al. 2020). Monitoring programmes should quickly collect reliable data over large areas to produce successive distribution snapshots which require cost-effective detection methods (Thorn et al. 2010, Parry and Peres 2015).

The performance of detection methods can be expressed as its ability to minimize false absences. False negatives have often been attributed to an intrinsic poor performance of the survey method (Harrington et al. 2008, Torrents-Ticó et al. 2017). However, local environmental conditions such as weather, substrate hardness, or habitat characteristics may also generate false negatives by indirectly reducing the performance of the survey method in detecting mammal species (Vine et al. 2009, Jeffress et al. 2011). These factors typically vary across space, especially when large regions are surveyed, and over time. Therefore, it is important to discriminate between methods exhibiting a consistently high capacity for detecting mammals from those featuring a context-dependent performance associated with their sensitivity to environmental variation.

Spatio-temporal factors influence mammal detection in two ways. Firstly, shifts in environmental conditions across space and over time bring about fluctuations in mammal activity (Zanón-Martínez et al. 2016, Jarnemo et al. 2017) and abundance (Sarmiento et al. 2010, Kontsiotis et al. 2013) which, in turn, affect the chances of detecting each species at different sites or attempts. Secondly, local environmental conditions such as substrate hardness, forest litter, or weather may affect the performance of the survey methods (Funston et al. 2010, Bartolommei et al. 2012). For example, camera lenses can get blurry due to the condensation of air moisture (Martin et al. 2017). Soft, clay or sandy soils may favor the probability of detecting mammals by conducting track surveys (Soto et al. 2012, Winterbach et al. 2016), whereas rain can wash away mammal tracks and scats during sign surveys (Schooely et al. 2012, Reid et al. 2013). Moreover, factors such as rainfall, vegetation cover, or the type of substrate may also affect the replication effort needed to accurately describe the composition of mammal assemblages (Bang et al. 2006, Conover and Linder 2009, Munari et al. 2011). Distinguishing between cases where detection only depends on species occurrence or abundance and cases where the spatio-temporal factors also affect detection is one major goal of large-scale occurrence surveys.

In monitoring programs of mammal occurrence over large regions, a single method or a unique set of detection methods are used in landscapes featuring different habitat characteristics or during sampling occasions long enough for observations to be recorded in different seasons (Cook and MacDonald 2004, Salom-Pérez et al. 2015). In these cases, it is implicitly assumed that the performance of selected survey methods is constant across space and over time. The potential bias introduced by spatio-temporal factors on species detection is sometimes acknowledged but not explicitly measured and subsequently corrected (Mortelliti and Boitani 2008, Espartosa et al. 2011); otherwise, bias is simply assumed as inevitable (Barea-Azcona et al. 2007). Assuming that a particular method will provide a homogeneous performance across space and over time or that its performance will be reduced (or improved) under certain circumstances might lead to unfounded decisions about method selection, eventually reducing the quality of mammal monitoring programs. Understanding their intrinsic advantages and drawbacks under different conditions permits an informed choice of survey methods (Mortelliti and Boitani 2008).

The performance of each survey method uses to be taxon-specific, some methods detecting particular species better than others. In multi-species or assemblage-level surveys, this problem is tackled by using several methods whose combination is deemed suited for the whole set of species present (Mazzolli et al. 2017). Finding a single effective method for all target species would be highly convenient because the simultaneous deployment of several detection methods is expensive and time-consuming. In this context, a survey method would be highly efficient if its description of local species occurrence closely approaches the outcome of a multi-method survey. We use this meaning for efficiency henceforth. Moreover, the length of survey periods in each locality tends to be inversely correlated with...
the number of localities or spatial replicates and, in turn, with the size of the area to be surveyed (Rossi et al. 2017). In large-scale mammal surveys, not every species actually occurring is detected during the typically short sampling sessions (Nader et al. 2011). In order to curtail this source of false negatives, several temporal replicates may be used to better approach true species occurrence at a single point in time during the much longer time frame defining the monitoring period. As considerable costs are incurred by repeating the survey, the ability of survey methods to detect species at the first attempt becomes another important component of method performance.

Little attention has been paid to explicitly assess and quantify the effect of spatio-temporal factors on mammal detection (Vine et al. 2009, Jeffress et al. 2011) and to compare the influence of spatio-temporal factors on the performance of different survey methods (Valente et al. 2018). The aim of this study is threefold. Firstly, we explore whether four widely employed detection methods differ in efficiency and whether any of them would describe true occurrence better than the others. Secondly, we test the null hypothesis that spatio-temporal factors do not affect the performance of survey methods used to detect species occurrence during large-scale mammal surveys. Thirdly, we examine the effect of landscape type on the number of temporal replicates needed to detect target species.

**Methods**

**Study area**

The study was carried out in a 900-km² region within the Guadiamar river basin, southwestern Spain (37°21’ N, 6°13’ W, Fig. 1A). The climate is temperate Mediterranean with rainfall occurring mostly from October to January (324 mm; 60% of annual precipitation). The study area encompasses three different landscapes diverging in relief, soil properties, vegetation cover, and land uses (Fig. 1B). In the uppermost area, Sierra Morena (SM) comprises a mosaic of Mediterranean forest, tree plantations, scrubland, and dehesas (pasturelands with open oak woodland; Campos et al. 2013). Soils are hard, thin, and poor, covering rugged terrain. Principal land uses involve forestry, livestockering, and big game.

Downstream, the Guadiamar agroecosystem (AGR) is a flat, broad valley with silt and clay soils. Natural vegetation is restricted to narrow strips of riparian forests and small, degraded, and scattered woodlots (Pereira and Rodriguez 2010). The dominant land use is agricultural (cereal crops, olive groves, and fruit tree plantations). In the lowermost area, Doñana (DO) is an even land with soft sandy soils occupied by a heterogeneous mosaic of scrubland, pine forests, pastureland, and crops.

**Detection methods**

**Camera traps.**—We used camera traps composed of a 35-mm analog compact camera (Canon Prima BF-9s) remotely triggered by animals stepping on a pressure pad. Pressure pads were wrapped with plastic for protection, and slightly buried in front of cameras at a distance of 1.5–3.0 m, and covered with a thin layer (0.5–1.0 cm) of the surrounding substrate and plant litter. Pads were hard-wired to the camera, and wires were also embedded in the ground. Cameras were placed at the height of 20 cm inside an open wooden case provided with a roof and overhanging eave, which protected the camera from rain and direct sunlight. In each site, camera traps were operated for ten consecutive days. Pads and cameras were checked for proper function on days 1, 2, 6, and 10. Mammal species were easily identified in pictures.

**Scent stations.**—Scent stations consisted of circular plates of sifted sand or earth 0.9 m in diameter and 2–4 cm thick (Linhart and Knowlton 1975). They were operated for two consecutive nights as subsequent effort does not significantly improve detection (Roughton and Sweeny 1982). We recorded visiting species and smoothed the surface the next morning. Track characteristics were unique for each target species in the study area and facilitated identification.

In plots with camera traps or scent stations, we used one of two olfactory attractants randomly distributed with equal proportion: plaster disks soaked with fatty acid scent (FAS; Roughton and Sweeny 1982; Pocatello Supply Depot, Pocatello, Idaho, USA) or a calcium sulfate prism of a similar volume sodden with catnip oil. In half of the plots, scents were reinforced with visual lures or with visual plus auditory stimuli. Further details on camera trap equipment, scent stations, and
the lack of effect of attractant types on detection have been described elsewhere (Suárez-Tangil and Rodríguez 2017).

**Sign surveys.**—We walked a non-pre-established trajectory across each sampling unit, approaching physiographic features favorable for finding tracks and scats of target mammal species. The survey effort per sampling unit was standardized at 90 min. For each species, we recorded the total number of signs, distinguishing between tracks and fecal remains. We counted tracks as separate records only if they belonged to different trails. For species using latrines, or producing pellet piles, aggregated fecal remains were considered a single record. Attributes of tracks and scats made species identification unequivocal in most cases, and any doubtful assignment to species was discarded.

**Sampling design**

We employed camera traps, scent stations, track surveys, and scat surveys to detect all 13 mammal species heavier than 0.8 kg known to be present in the regional species pool. According to Palomo et al. (2007), the mammal assemblage is composed of two lagomorphs (European rabbit, Oryctolagus cuniculus L.; Iberian hare, Lepus granatensis Rosenhauer), two ungulates (wild boar, Sus scrofa L.; red deer, Cervus elaphus L.), and nine carnivores (red fox, Vulpes vulpes L.;...
common genet, Genetta genetta L.; Egyptian mongoose, Herpestes ichneumon L.; Eurasian badger, Meles meles L.; stone marten, Martes foina Erxleben; Eurasian otter, Lutra lutra L.; European polecat, Mustela putorius L.; Iberian lynx, Lynx pardinus Temminck; wildcat, Felis silvestris Schreber.

We placed eight 4-km² sampling units on the UTM projection grid in each of the three different landscapes (Fig. 1B), so that units were two kilometers apart from their nearest neighbor. In each sampling unit, eight detection plots were spaced at a mean distance of 537 m (range 293–2485 m). Four scent stations and four camera traps were randomly assigned to these eight plots (Fig. 1C). We assumed that species occupancy was constant in each plot throughout the study period. We replicated the survey four times, at six-month intervals, during late spring and late autumn of two consecutive years. During each session, field surveys lasted for six weeks. Sign surveys (including track and scat surveys, see Detection methods) were carried out once per sampling unit and session (Fig. 1C).

**Data**

We considered species identification by each detection method as a binary variable for each species and session. We defined landscape (SM, AGR, and DO) and season (Spring, Autumn) as spatio-temporal factors representing variation in habitat characteristics, physiographic features (e.g., ruggedness or substrate hardness), and weather. The factor of interest was the survey method, which had four levels (camera, scent, track, and scat). To assess the effect of spatio-temporal factors on species detection, we chose two attributes of method performance as response variables: the probability of detection (hereafter POD, MacKenzie et al. 2002); and the replication effort, that is, the number of sampling sessions needed for the first detection.

**Analyses**

We employed occupancy models to analyze the influence of spatio-temporal factors on the POD for each mammal species. These models simultaneously estimate the probabilities of occupancy and detection (MacKenzie et al. 2002). As we were interested in POD and assumed no change in species occurrence during the study period, the probability of occupancy was kept constant in all models (MacKenzie et al. 2006). To account for sources of false negatives derived intrinsically from the survey methods, we fitted occupancy models for each method separately. POD was estimated for each level of landscape and season. Single-species, single-season occupancy models (MacKenzie et al. 2002) were fitted using the software PRESENCE v10.8 (Hines 2006).

Efficiency.—All else being equal, abundant and more active mammal species might be easier to detect than rare species (Steinbeiser et al. 2019). To control the effect of this source of species-specific variation on POD, we assessed method efficiency by analyzing how close the POD depicted by a single method was to the outcome of a multi-method survey, which was expected to better resemble actual species occurrence. Specifically, we calculated efficiency as the ratio between the POD estimated for the focal method and the POD estimated from the detection histories resulting from the joint use of all four survey methods, that is, the multi-method survey. By doing this, we aimed to partition the variation associated with mammal abundance or activity, which would be equally captured by both single-method and multi-method surveys, and the variation attributed to pure method performance on mammal detection, which would be represented by the magnitude of the single-method to multi-method POD ratio.

Influence of spatio-temporal factors on efficiency.—To explicitly analyze the influence of spatio-temporal factors on method efficiency, we used generalized additive models for location, scale, and shape (GAMLSS; Rigby and Stasinopoulos 2005) applying the zero-and-one inflated distribution, which is a mixture between a beta distribution and a Bernoulli distribution (Ospina and Ferrari 2010). This distribution allows modeling data that are measured on a continuous scale on the closed interval [0, 1]; as this interval includes zero and one, the distribution is suitable for modeling proportions. The main effect of method performance and its interaction with spatio-temporal factors were explicitly tested in models where efficiency was the response variable. We selected models with the lowest AIC value (Burnham and Anderson 2002). GAMLSS were
Table 1. Difference between the probability of detection (POD) estimated for the focal method and the POD estimated from the detection histories resulting from the joint use of all four survey methods (ΔPOD) of target mammal species.

| Survey method   | Species          | SM  | AGR | DO  | ΔPOD  | ΔPOD  |
|-----------------|------------------|-----|-----|-----|-------|-------|
|                 |                  |     |     |     | Spring| Autumn|
| Camera traps    | Common genet     | 0.32| 0.40| 0.35| 0.21  | 0.28  |
|                 | Egyptian mongoose| 0.50| 0.10|     |       |       |
|                 | Eurasian badger  | 0.50| 0.89| 0.63| 0.68  | 0.44  |
|                 | Eurasian otter   | 0.50| 0.84|     | 0.92  | 0.56  |
|                 | European polecat | 0.05| 0.00| 0.03| 0.02  | 0.02  |
|                 | European rabbit  | 0.91| 0.54| 0.78| 0.64  | 0.67  |
|                 | Iberian hare     | 0.43| 0.67| 0.53| 0.39  | 0.61  |
|                 | Iberian lynx     |     |     |     | 0.46  | 0.02  |
|                 | Red deer         | 0.88|     | 0.16| 0.75  | 0.77  |
|                 | Red fox          | 0.91| 0.85| 0.97| 0.94  | 0.92  |
|                 | Stone marten     | 0.36|     |     | 0.33  | 0.04  |
|                 | Wild boar        | 0.58|     | 0.25| 0.29  | 0.80  |
|                 | Wildcat          | 0.27| 0.27| 0.03| 0.29  | 0.06  |
| Scent stations  | Common genet     | 0.40| 0.40| 0.53| 0.57  | 0.43  |
|                 | Egyptian mongoose| 0.53| 0.10| 0.57| 0.88  | 0.23  |
|                 | Eurasian badger  | 0.47| 0.80| 0.54| 0.62  | 0.42  |
|                 | Eurasian otter   | 0.50| 0.84|     | 0.92  | 0.56  |
|                 | European polecat | 0.05| 0.03| 0.00| 0.02  | 0.02  |
|                 | European rabbit  | 0.48| 0.06| 0.19| 0.13  | 0.25  |
|                 | Iberian hare     | 0.43| 0.44| 0.56| 0.22  | 0.00  |
|                 | Iberian lynx     |     |     |     | 0.02  | 0.02  |
|                 | Red deer         | 0.88|     | 0.13| 0.73  | 0.77  |
|                 | Red fox          | 0.41| 0.60| 0.70| 0.64  | 0.63  |
|                 | Stone marten     | 0.36|     |     | 0.33  | 0.04  |
|                 | Wild boar        | 0.58|     | 0.25| 0.31  | 0.78  |
|                 | Wildcat          | 0.24| 0.27| 0.03| 0.27  | 0.06  |
| Track surveys   | Common genet     | 0.34| 0.00| 0.10| 0.17  | 0.07  |
|                 | Egyptian mongoose| 0.12| 0.10| 0.06| 0.31  | 0.56  |
|                 | Eurasian badger  | 0.12| 0.30| 0.04| 0.17  | 0.10  |
|                 | Eurasian otter   | 0.04| 0.43|     | 0.52  | 0.34  |
|                 | European polecat | 0.00| 0.03| 0.03| 0.00  | 0.04  |
|                 | European rabbit  | 0.19| 0.19| 0.00| 0.12  | 0.15  |
|                 | Iberian hare     | 0.30| 0.28| 0.19| 0.44  | 0.17  |
|                 | Iberian lynx     |     |     |     | 0.43  | 0.00  |
|                 | Red deer         | 0.02|     | 0.07| 0.10  | 0.10  |
|                 | Red fox          | 0.12| 0.22| 0.03| 0.11  | 0.11  |
|                 | Stone marten     | 0.36|     |     | 0.31  | 0.06  |
|                 | Wild boar        | 0.10|     | 0.03| 0.08  | 0.13  |
|                 | Wildcat          |     |     |     | 0.00  | 0.00  |
| Scat surveys    | Common genet     | 0.50| 0.00| 0.60| 0.11  | 0.54  |
|                 | Egyptian mongoose| 0.53| 0.10| 0.84| 0.82  | 0.06  |
|                 | Eurasian badger  | 0.40| 0.89| 0.63| 0.66  | 0.48  |
|                 | Eurasian otter   | 0.12| 0.03| 0.16|     | 0.16  |
|                 | European polecat | 0.00| 0.03| 0.03| 0.00  | 0.04  |
|                 | European rabbit  | 0.25| 0.00| 0.03| 0.07  | 0.04  |
|                 | Iberian hare     | 0.21| 0.11| 0.15| 0.20  | 0.10  |
|                 | Iberian lynx     |     |     |     | 0.43  | 0.02  |
|                 | Red deer         | 0.54|     |     | 0.42  | 0.48  |
|                 | Red fox          | 0.06| 0.22| 0.51| 0.25  | 0.20  |
|                 | Stone marten     | 0.09|     |     | 0.00  | 0.02  |
|                 | Wild boar        | 0.27| 0.19|     | 0.25  | 0.30  |
|                 | Wildcat          | 0.27| 0.27| 0.03| 0.29  | 0.06  |

Note: POD values were derived from competitive occupancy models.
† Overestimation of POD due to the detection of the species in a single site during two or more successive sessions.
‡ The POD estimate for the focal method was (paradoxically) higher than that of the multi-method survey. Blank cells represent cases where the species was not detected by the focal method and the POD could not be estimated.
fitted in R v3.5.3 (R Development Core Team 2019) using the gamlss package (Rigby and Stasinopoulos 2005).

Replication effort.—We used survival analysis to assess differences in the replication effort (Garrett et al. 2008, Bischof et al. 2014). Specifically, for each method and species, we used Cox proportional hazards models (Cox 1972) to compute hazard ratios (hereafter HR) and compared HR between landscape types. To control the variation in replication effort due to species-specific differences in relative abundance or activity, we compared the HR obtained for each detection method and the HR from the joint use of all the methods. Cox proportional hazards models were fitted in R, using package survival (Therneau 2005) and package survminer (Kassambara and Kosinski 2018).

RESULTS

For track surveys and scat surveys, the mean raw difference between the POD estimated for the focal method and the POD estimated for the multi-method survey was lower than for camera traps and scent stations (Table 1).

Efficiency

Between-method differences in efficiency were significant across landscapes ($F = 6.78$, df = 3, $P < 0.001$) and between seasons ($F = 4.42$, df = 3, $P = 0.008$). Differences in efficiency between track surveys and camera traps were significant (effect of landscape $\Delta$Efficiency = 0.31, $P < 0.001$; effect of season $\Delta$Efficiency = 0.29, $P = 0.013$). Differences in efficiency between track surveys and scent stations were significant only across landscapes ($\Delta$Efficiency = 0.25, $P = 0.012$).

Influence of spatio-temporal factors on efficiency

Two sets of GAMLSS were fitted for each spatio-temporal factor. Including the interaction term between each spatio-temporal factor and detection method did not improve the fit of main effect models (Table 2), in contrast with what would be expected from a significant effect of spatio-temporal factors on detection. Nevertheless, selected models revealed a significant effect of the detection method on efficiency (Table 2). For both landscape and season, the efficiency of track surveys and scat surveys was significantly higher than that of camera traps. In contrast, the efficiency of scent stations was not significantly different from that of camera traps.

Replication effort

Cox proportional hazard models revealed that species-specific variations in abundance or activity, which are assumed to be associated with landscape type through species-habitat relationships, affected the effort needed to detect target mammal species (Appendix S1: Table S1). However, this effect was not consistent among survey methods (Table 3). Comparing with the HR obtained from the multi-method survey (Appendix S1: Table S1), significant differences in replication effort were found for Iberian hare, red deer, and Egyptian mongoose (Table 3). The replication effort required to detect target species with camera traps was the most dissimilar to that of using all four detection methods simultaneously (Table 3, Appendix S1: Table S1). By employing scent stations, only the lower replication effort needed to detect the Iberian hare in AGR agreed with the multi-method approach. Track surveys best matched the replication effort needed to detect the target species employing the multi-method survey. Only in two cases, the HR for track surveys were different from those found for the multi-method survey: the higher effort needed to detect red deer in DO and the lower replication effort needed to detect the Iberian hare in DO (Table 3). Using scat surveys, a higher replication effort was needed to detect red deer in DO, and a lower replication effort was needed to detect Iberian hare in DO. However, unlike the multi-method approach, no significant differences in the needed replication effort were found in AGR for any species (Table 3).

DISCUSSION

Spatial heterogeneity in habitat characteristics or temporal variability in meteorological conditions may affect population abundance or individual activity and, eventually, the probability of detection. This external component of variation in mammal detection should be examined and controlled for before assessing whether detection by each survey method is consistent under different environmental contexts, as a result of its intrinsic performance. This assessment involves...
comparing the occurrence described by the survey method under evaluation with actual species occupancy. True occupancy, however, could only be determined by a survey method able to detect the species without error, an ideal method that hardly exists. Assessing occurrence with a single detection method also makes unfeasible isolating the intrinsic component of performance from the external component associated with mammal abundance and activity. For example, Jeffress et al. (2011) used a single method for evaluating the influence of spatio-temporal factors on the performance of sign surveys to detect North American river otters (*Lontra canadensis*). Other studies have compared the efficiency of different methods for detecting a single (Vine et al. 2009) or multiple mammal species (Valente et al. 2018). However, the potential influence of the species relative abundance or activity on method efficiency was not considered. Whenever possible, we propose using the combined outcome of several detection methods (four in our study) as the best estimate of true species occurrence. Species-specific variations in relative abundance and activity of target mammals across space and over time equally affect all survey methods. Therefore, controlling underlying differences in probability of detection by contrasting the efficiency of each method with the efficiency resulting from the joint use of all survey methods may help to improve future assessments of the consistency of method performance under contrasting environmental conditions.

Our results support the hypothesis that spatio-temporal factors did not significantly alter the efficiency of the methods we compared and that, for each survey method, estimates of mammal occurrence are comparable with no further correction between the environmental conditions we tested. However, we also found that the effect of variables associated with landscape properties on the replication effort needed to detect target species greatly varied between methods. For most species, the efficiency and replication effort needed to detect mammals employing track surveys matched the corresponding efficiency and replication of the multi-method survey. Track surveys have been sometimes discarded for monitoring mammal assemblages in Mediterranean ecosystems because of potential issues related to environmental conditions (Barea-Azcón et al. 2007). Our results clearly show that track surveys were a very efficient methodology for detecting mammals over large regions. Indeed, track surveys have been successfully employed in the Mediterranean and other biomes (see Espartosa et al. 2011, Ferreras et al. 2011, Keeping 2014 for some examples). Scat surveys also detected most species quickly and, although the identification of certain species might be complicated even for experienced observers (Harrington et al. 2010), this methodology has proved useful for monitoring mammals in large areas (e.g., Mangas et al. 2008, Karanth et al. 2011, Carreras-Duro et al. 2016). Our results support that active searching of sites where mammal tracks or scats are

### Table 2. Effect of spatio-temporal factors on detection method efficiency.

| Models                  | df | AIC  | ΔAIC | Effect | Coefficient | SE  | P       |
|-------------------------|----|------|------|--------|-------------|-----|---------|
| Season                  |    |      |      |        |             |     |         |
| Survey method           | 7  | 161.61 | 0.00 | Scent stations | 0.24 | 0.38 | 0.525   |
|                         |    |      |      | Track surveys  | 1.51 | 0.37 | *<0.001***|
|                         |    |      |      | Scat surveys   | 1.22 | 0.37 | *<0.01** |
| Survey method × season  | 11 | 166.56 | 4.95 | Scent stations | 0.37 | 0.34 | 0.276   |
|                         |    |      |      | Track surveys  | 1.76 | 0.34 | *<0.001***|
|                         |    |      |      | Scat surveys   | 1.24 | 0.35 | *<0.001***|
| Landscape               |    |      |      |        |             |     |         |
| Survey method           | 7  | 191.45 | 0.00 | Scent stations | 0.37 | 0.34 | 0.276   |
|                         |    |      |      | Track surveys  | 1.76 | 0.34 | *<0.001***|
|                         |    |      |      | Scat surveys   | 1.24 | 0.35 | *<0.001***|
| Survey method × landscape| 15 | 200.10 | 8.65 |        |             |     |         |

**Notes:** As probability of detection was estimated separately for season and landscape, two sets of GAMLSSs were fit (one for season and one for landscape). Models ordered by the fit statistic AIC. Only parameter estimates of the selected models are shown. The method camera traps is included in the intercept. AIC is Akaike Information Criterion.
Table 3. Hazard ratios, HR (95% CI) derived from Cox proportional hazard models to compare the replication effort needed to detect target species.

| Survey method | Species          | AGR  | DO  |
|---------------|------------------|------|-----|
| Camera traps  | Common genet     | 0.4  | 1.3 |
|               | Egyptian mongoose| 0.3  | 0.3 |
|               | Eurasian badger  | 0.3  | 0.3 |
|               | Eurasian otter   | 7.3  | 7.5 |
|               | European polecat | 5.4  | 1.0 |
|               | European rabbit  | 0.5  | 0.5 |
| Scent stations| Common genet     | 0.2  | 0.6 |
|               | Egyptian mongoose| 0.5  | 1.0 |
|               | Eurasian badger  | 0.5  | 1.5 |
|               | Eurasian otter   | 3.0  | 2.3 |
|               | European polecat | 4.9  | 1.3 |
|               | European rabbit  | 6.37 | 1.6 |
|               | Iberian hare     | 0.4  | 0.3 |
|               | Red deer         | 0.6  | 0.3 |
|               | Red fox          | 1.0  | 0.3 |
|               | Wild boar        | 0.7  | 0.7 |
| Track surveys | Common genet     | 0.4  | 2.3 |
|               | Egyptian mongoose| 0.0  | 3.7 |
|               | Eurasian badger  | 0.2  | 1.0 |
|               | Eurasian otter   | 4.9  | 1.3 |
|               | European polecat | 1.0  | 1.4 |
|               | European rabbit  | 6.37 | 0.6 |
|               | Iberian hare     | 0.4  | 0.6 |
|               | Red deer         | 0.6  | 1.7 |
|               | Red fox          | 0.7  | 0.3 |
|               | Wildcat          | 0.7  | 0.7 |
| Scat surveys  | Common genet     | 0.4  | 0.3 |
|               | Egyptian mongoose| 0.5  | 0.7 |
|               | Eurasian badger  | 2.7  | 0.7 |
|               | Eurasian otter   | 2.8  | 2.8 |
|               | European polecat | 1.1  | 0.1 |
|               | European rabbit  | 1.8  | 0.2 |
|               | Iberian hare     | 0.6  | 0.1 |

Notes: Values of HR < 1 indicate that in the focal landscape more sessions are needed to detect species than in Sierra Morena (SM, reference landscape). In contrast, values of HR > 1 indicate that in the focal landscape the species is detected earlier than in SM. Significant differences between SM and the focal landscape are marked in bold. Abbreviations are AGR, Guadianar agroecosystem and DO, Doñana. Blank cells represent cases where the focal method did not detect the species or that it was detected only once during the study period. Stone marten and Iberian lynx were excluded from the analyses because they were detected in just one landscape.
seem to require considerable survey effort to achieve a reliable description of mammal assemblages, which is supported by our results. The use of camera traps and scent stations yielded occurrence maps that were more dissimilar to those derived from the multi-method survey than occurrence maps derived from sign surveys. In other words, recording the composition of the mammal assemblage with camera traps and scent stations required a higher replication effort as compared with track or scat surveys. In large-scale field surveys, the trade-off between extension and intensity often entails logistical constraints limiting the number of cameras or stations deployed simultaneously and the duration of their operation period, thus decreasing the probability of detecting a fraction of occurring mammal species. In our case, the need to detect as many species as possible, while minimizing survey effort, points to sign surveys as suitable tools for monitoring the composition of mammal assemblages over large and heterogeneous regions.

**CONCLUSIONS**

Biodiversity monitoring requires accurate and reliable data. Large-scale mammal surveys often cover landscapes encompassing different habitats and may last for long periods with contrasting meteorological conditions. After controlling for variations in mammal relative abundance or activity associated with landscape and season, the effect of spatio-temporal factors on the performance of detection methods was small. Likewise, after controlling for species-specific differences in detection, we found a small and inconsistent effect of landscape type on the replication effort needed to detect the targeted species. These results suggest that between-method differences in mammal detection are genuine, and the effect of major spatio-temporal factors could be ruled out, which might benefit a more general interpretation of our conclusions. Additionally, results suggest that differences in the composition of mammal communities across seasons or different landscapes of a larger heterogeneous region, as depicted from a single method or a set of survey methods, have ecological meaning and are not mere artefacts resulting from variable detection performance under different environmental conditions. As track surveys proved to be the most efficient and fastest method for detecting mammal species and were barely influenced by spatio-temporal factors, we recommend the use of track surveys to monitor the composition of mammal assemblages in Mediterranean ecosystems. We also recommend accounting for spatio-temporal factors affecting species detection in pilot studies used to select the most suitable survey method, in order to explore whether our findings are general and in the hope that doing so the confidence in the results of mammal monitoring programs will improve.

**ACKNOWLEDGMENTS**

We thank Miguel Delibes, Juan Carlos Rivilla, Sonia Alís, and many owners who allowed us to work in their lands. We are also grateful to two anonymous reviewers for their helpful comments. The study was funded by grant CGL2016-75205-R from the Spanish National Research Agency (AEI), Junta de Andalucía (Consejería de Medio Ambiente; Consejería de Innovación, Ciencia y Empresa, grant P06-RNM-1903), and the European Regional Development Fund (FEDER). Bruno David Suárez-Tangil acknowledges the financial support of the Tatiana Pérez de Guzmán el Bueno Foundation. The authors declare that they have no conflict of interest.

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