Conservation Methods

Use of ambiguous detections to improve estimates from species distribution models

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Abstract: _As large carnivores recover throughout Europe, their distribution needs to be studied to determine their conservation status and assess the potential for human-carnivore conflicts. However, efficient monitoring of many large carnivore species is challenging due to their rarity, elusive behavior, and large home ranges. Their monitoring can include opportunistic sightings from citizens in addition to designed surveys. Two types of detection errors may occur in such monitoring schemes: false negatives and false positives. False-negative detections can be accounted for in species distribution models (SDMs) that deal with imperfect detection. False-positive detections, due to species misidentification, have rarely been accounted for in SDMs. Generally, researchers use ad hoc data-filtering methods to discard ambiguous observations prior to analysis. These practices may discard valuable ecological information on the distribution of a species. We investigated the costs and benefits of including data types that may include false positives rather than discarding them for SDMs of large carnivores. We used a dynamic occupancy model that simultaneously accounts for false negatives and positives to jointly analyze data that included both unambiguous detections and ambiguous detections. We used simulations to compare the performances of our model with a model fitted on unambiguous data only. We tested the 2 models in 4 scenarios in which parameters that control false-positive detections and true detections varied. We applied our model to data from the monitoring of the Eurasian lynx_ (Lynx lynx) _in the European Alps. The addition of ambiguous detections increased the precision of parameter estimates. For the Eurasian lynx, incorporating ambiguous detections produced more precise estimates of the ecological parameters and revealed additional occupied sites in areas where the species is likely expanding. Overall, we found that ambiguous data should be considered when studying the distribution of large carnivores through the use of dynamic occupancy models that account for misidentification._

Keywords: false positives, large carnivores, lynx, occupancy models, species imperfect detection

Uso de Detecciones Ambiguas para Mejorar las Estimaciones a partir de Modelos de Distribución de Especies

Resumen: _Conforme los carnívoros mayores se recuperan en toda Europa, su distribución requiere ser estudiada para determinar su estado de conservación y para evaluar el potencial de conflictos entre humanos y carnívoros. Sin embargo, el monitoreo eficiente de muchas especies de carnívoros mayores es complicada debido a su rareza, comportamiento elusivo y las grandes extensiones de su ámbito de hogar. Su monitoreo_

puede incluir avistamientos oportunistas por parte de los ciudadanos, además de los censos diseñados. Pueden ocurrir dos tipos de errores de detección en dichos métodos de monitoreo: negativos falsos y negativos positivos. La detección de los falsos negativos puede justificarse en los modelos de distribución de especies (MDE) que manejan la detección imperfecta. La detección de falsos positivos por causa de la identificación errónea rara vez se justifica en los MDE. Los investigadores usan generalmente métodos con filtración de datos ad hoc para descartar las observaciones ambiguas previo al análisis. Estas prácticas pueden descartar información ecológica variable sobre la distribución de una especie. Investigamos los costos y beneficios de la inclusión de tipos de datos que podrían contener falsos positivos en lugar de descartarlos de los MDE para carnívoros mayores. Usamos un modelo dinámico de ocupación que justificó simultáneamente los falsos positivos y falsos negativos para analizar en conjunto los datos que incluían tanto las detecciones no ambiguas como las ambiguas. Usamos simulaciones para comparar el desempeño de nuestro modelo con el de un modelo ajustado solamente para datos no ambiguos. Probamos los dos modelos en cuatro escenarios en los que variaron los parámetros que controlan la detección de falsos positivos y de detecciones verdaderas. Aplicamos nuestro modelo a datos del monitoreo del lince euroasiático (Lynx lynx) en los Alpes. La suma de las detecciones ambiguas incrementó la precisión de las estimaciones de los parámetros. Para el lince euroasiático, la incorporación de las detecciones ambiguas produjo estimaciones más precisas de los parámetros ecológicos y reveló sitios ocupados adicionales en áreas en donde la especie probablemente se esté expandiendo. En general, encontramos que los datos ambiguos deberían ser considerados cuando se estudia la distribución de carnívoros mayores por medio del uso de modelos dinámicos de ocupación que justifican la identificación errónea.

Palabras Clave: carnívoros mayores, detección imperfecta de especies, lince, modelos de ocupación, positivos falsos

摘要: 随着欧洲大型食肉动物的恢复, 我们需要研究这些物种的分布以确定它们的保护现状, 并评估人兽冲突的可能性。然而, 由于大型食肉动物的稀有性、回避行为和较大的活动范围, 对它们进行有效监测困难重重。大型食肉动物的监测除了设计调查外, 还可以包含公民的偶然目击。这样的监测方案可能出现两类检测误差: 假阴性和假阳性。假阴性的监测结果可用于物种分布模型分析, 该模型可处理有缺陷的监测。而因物种鉴定错误产生的假阳性结果在物种分布模型中却很少被考虑在内。通常情况下, 研究者在分析前会用特定的数据过滤方法来去除不确定的观察数据。这种做法也可能丢掉对物种分布有价值的生态学信息。我们研究了保留可能含有假阳性发现的数据类型 (而不是丢弃这些数据) 对大型食肉动物物种分布模型的利弊。我们利用同时考虑假阴性和阳性的动态占有模型, 共同分析了包含确定发现和不确定发现的数据。通过模拟, 我们比较了这个模型和仅用真实数据拟合的模型的表现。我们选择了不同的控制假阳性和真阳性的参数, 在四种情况下检验了这两个模型。我们还将这一模型应用于欧洲阿尔卑斯山脉的欧亚猞猁 (Lynx lynx) 的监测数据, 加入不确定的发现数据可以提高参数估计的精确度。对欧亚猞猁来说, 加入不确定的发现可以对生态学参数作出更精确的估计, 揭示这个物种的分布范围可能正在扩张。总之, 我们的研究表明, 在研究大型食肉动物的分布时, 可以用考虑到物种鉴定错误的动态占有模型来利用不确定的数据。**翻译: 胡怡思; 审校: 聂永刚**

关键词: 假阳性, 大型食肉动物, 猞猁, 占据模型, 物种不充分检测

Introduction

The distribution and abundance of large carnivores in many parts of the world has been declining for centuries because of habitat loss and human persecution (Ripple et al. 2014). Thanks to active conservation measures, several species of large carnivores have been recently expanding their ranges substantially in Europe. As a result, most European countries currently host at least 1 viable population of a large predator (Chapron et al. 2014). This expansion has led to the emergence of conflicts with humans (Ripple et al. 2014). In this context, accurate distribution mapping (i.e., species distribution models [SDMs]) (Elith & Leathwick 2009) is essential for determining conservation status and recovery success (IUCN 2012); targeting potential areas of occurrence; understanding large carnivore range dynamics; identifying possible areas for future population establishment

(Chapron et al. 2014); and mitigating conflicts associated with the recovery of large carnivores (Guillera-Arroita et al. 2015), for example, depredation of livestock by wolves (Marucco & Mcintire 2010). However, carnivore rarity, elusive behavior, and low densities render efficient monitoring difficult (Ripple et al. 2014).

The monitoring of large carnivores in Europe relies on several survey methods implemented by professionals and members of the public (citizens). In particular, citizen participation increases the ability to survey large areas over extended periods, an effort that would be costly if done by professionals only (Molinari-Jobin et al. 2018). A primary goal of citizen science (CS) is to produce reliable data and information that scientists or decision makers can use (McKinley et al. 2017), and it is becoming an important tool with which to study the distribution, abundance, and species richness of plants and animals (Silvertown 2009; Dickinson et al. 2012). However,

CS-generated data present potential quality problems, especially when the goal is to build SDMs.

Difficulty detecting large carnivores means animals can be missed at sites where they are present (i.e., producing false-negative observations). Occupancy models were developed to deal with false-negative errors (Guillera-Arroita 2017) and are recommended for analyzing CS data (Isaac et al. 2014). Although data sets produced by CS are valuable (Kosmala et al. 2016), professionals are better able to detect or identify species of interest, which diminishes the risk of identification errors (Fitzpatrick et al. 2009). False positives can occur when a species is detected through misidentification at a site where it does not occur (Miller et al. 2011). Recent studies have demonstrated the importance of accounting for misidentification for SDMs (Miller et al. 2011, 2013; Chambert et al. 2015). Ignoring misidentification may lead to overestimating a species range (Royle & Link 2006; McClintock et al. 2010).

Usually large carnivores are surveyed with indirect methods, for example, observations of tracks, scat, and prey remains or use of camera traps (Molinari-Jobin et al. 2018). Observations are then filtered by experts to assess the reliability of evidence of the observed presence. Recent studies of the distribution of European large carnivores have been based on only reliable observations, that is, those remaining after discarding ambiguous detections and validation by experts (Molinari-Jobin et al. 2018). This means that some observations are discarded, even though they may contain relevant ecological information on the species distribution. This raises the question of whether this information can somehow be extracted and made useful in the context of SDMs.

We investigated the pros and cons of removing ambiguous detections in SDMs of large carnivores versus keeping all records and formally accounting for misidentification. We used a dynamic occupancy model that accounts for both false-negative and false-positive errors (Miller et al. 2011, 2013) to jointly analyze unambiguous and ambiguous detections. To assess the performance of this approach, we performed a simulation study in which we compared the analysis of unambiguous and ambiguous detections with the use of unambiguous detections only.

We applied these methods to an SDM of the Eurasian lynx (*Lynx lynx*) in the European Alps (Molinari-Jobin et al. 2018). We expected improved precision in ecological parameter estimates when all data were included in an analysis, despite having to accommodate additional nuisance parameters to deal with misidentification.

Methods

Occupancy Model Accounting for Misidentification

Dynamic occupancy models allow estimation of occupancy and its temporal dynamics as a function of local extinction and colonization probabilities while accounting for imperfect species detection (MacKenzie et al. 2003). These models can be formulated as state–space models to separate the state process (i.e., whether or not a species is present at a site and how presence changes over time) from the observational process (i.e., whether a species is observed at a site during a given period depending on whether or not it was actually present) (Royle & Kéry 2007). We defined $z_{i,1}$ as the initial latent occurrence state of site i ($z = 1$, presence; $z = 0$, absence) and $z_{i,t}$ as the latent state for site i at time t. The state process is initiated by the initial occupancy probability ($\psi_{i,1}$) for site i and governed by colonization probability ($\gamma_{i,t}$) (the probability that a site i that is not occupied at time t will become occupied at time $t + 1$) and extinction probability ($\varepsilon_{i,t}$) (the probability that an occupied site i at time t will become unoccupied at time $t + 1$). We modeled $z_{i,1}$ as a draw from a Bernoulli distribution with probability $\psi_{i,1}$. All subsequent latent states $z_{i,t}$ for $t > 1$ were draws from another Bernoulli distribution that combines both possible extinction and colonization events:

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}(1 - \varepsilon_{i,t}) + (1 - z_{i,t})\gamma_{i,t}). \quad (1)$$

If a site is occupied in year (or season) t, it will still be occupied with probability $1 - \varepsilon_{i,t}$ or if it is unoccupied, it will become occupied with probability $\gamma_{i,t}$. Each year (or season), a site is surveyed several times (j) within a year or season. Site occupancy models rely on satisfaction of the site-closure assumption, whereby the latent occurrence state of a site does not change within a sampling season, whereas occupancy dynamics (colonization and extinction) happen between years (or seasons).

In addition to the state process, the observation process leads to the data $y_{i,j,t}$: the observed state of site i during a secondary survey j within year (or season) t. Hereafter, we do not use the indices when possible to ease reading of the model parameters. Here, $y = 0$ denotes no detection, $y = 1$ an unambiguous detection, and $y = 2$ an ambiguous detection. To account for unambiguous and ambiguous detections, we followed the formulation of Miller et al. (2013). We defined an additional parameter $d_{i,j,t}$ that had a value of 1 if any detection (ambiguous or unambiguous) was made at site i during survey j within year t and a value of 0 if there were no detections. For occupied sites, by definition, $d = 1$ and denoted a true detection. For unoccupied sites, $d = 1$ was a false-positive detection. For both occupied and unoccupied sites, $d = 0$ meant no detection and thus $y = 0$. At an occupied site, the possible observations were no detection ($y = 0$), unambiguous detection ($y = 1| d = 1$), or ambiguous detection ($y = 2| d = 1$). For occupied sites, the probability of a true detection (i.e., $d = 1$) during a secondary sampling occasion (or survey) was defined as $P(d = 1| z = 1)$ (hereafter p_{11}). The probability that a true detection will be classified as unambiguous was

$P(y = 1 | d = 1)$ (hereafter b). The probability of an unambiguous detection was $p_{11}b$, and the probability for an ambiguous detection (i.e., $y = 2$) for an occupied site was $p_{11}(1 - b)$. For unoccupied sites (i.e., $z = 0$), by definition, unambiguous detections ($y = 1 | d = 1$) did not occur; thus, the only possible observations were an ambiguous detection ($y = 2 | d = 1$), which in this case is a false positive, or no detection ($y = 0$). The probability of a false positive detection (i.e., $d = 1$) occurring at an unoccupied site i during a secondary sampling occasion (or survey) j was $P(d = 1 | z = 0)$ (hereafter p_{10}). Then the probabilities, unconditional on state z of a site, of recording the 3 possible observed states (y) were

$$P(y = 0) = P(z = 1) P(d = 0 | z = 1)$$
$$+ P(z = 0) P(d = 0 | z = 0) = \psi(1 - p_{11})$$
$$+ (1 - \psi)(1 - p_{10}) \text{ for no detection;}$$
$$P(y = 1) = P(z = 1) P(d = 1 | z = 1) P(y = 1 | d = 1)$$
$$= \psi p_{11} b \text{ for unambiguous detection; and}$$
$$P(y = 2) = P(z = 1) P(d = 1 | z = 1) P(y = 2 | d = 1)$$
$$+ P(z = 0) P(d = 1 | z = 0) = \psi p_{11}(1 - b)$$
$$+ (1 - \psi) p_{10} \text{ for ambiguous detection.}$$

Simulations

We conducted a simulation to examine the performance of a dynamic occupancy model that accounted for possible false positives (model unambiguous or ambiguous [MUA]) relative to a dynamic occupancy model that accounted only for false negatives (fitted with unambiguous data only) (model unambiguous [MU]). To assess the ability of both models to estimate ecological parameters, we tested 4 scenarios in which parameters that control false-positive detections and true detections varied (Table 1).

Because the ecological parameters have an influence on the amount of detections produced, occupancy probability was either high or low. In the high occupancy scenario, we set the initial occupancy probability ψ_1 at 0.8, the colonization probability γ at 0.4, and extinction probability at 0.1 to maintain a high occupancy probability. This scenario corresponds to a fairly well-established species reflected by its high occupancy probability across time. In the low occupancy scenario, we set the initial occupancy probability ψ_1 at 0.1, the colonization probability γ at 0.1, and extinction probability at 0.1 to maintain a low occupancy probability. This scenario corresponds to a rare species with a low occupancy probability across time.

Detection parameters also influence the amount of false-positive and true-positive detections. True detections are controlled by p_{11} and b. Therefore, in both high and low occupancy scenarios, we considered 2 situations

in which b was either high (i.e., set at 0.8) or low (i.e., set at 0.5), for a total of 4 scenarios. For all scenarios, we set p_{11} at 0.4. When $b = 0.8$, most of the true detections were classified as unambiguous. This scenario corresponds to monitoring of a species that is not easily mistaken for another or monitoring conducted by people trained to recognize accurately the presence signs of the species. When $b = 0.5$, a larger part of the true detections was classified as ambiguous. This scenario corresponds to the monitoring of a species that can easily be mistaken or done by untrained people, for instance from the general public. The amount of false-positive detections was controlled by p_{10}. In all 4 scenarios, we looked at how the models performed under 7 different values of p_{10} (range 0.01–0.3), for a total of 28 different simulation scenarios. Finally, because our main objective was to assess the effect of accounting for ambiguous data, environmental variation was not included in our simulations. The high occupancy high b scenario is referred to as HH; the high occupancy low b scenario is HL; the low occupancy high b scenario is LH; and the low occupancy low b is LL.

In our simulations, we generated data for 100 sites over 5 years and 3 surveys. To remain realistic in the simulations, the number of surveys mimicked the case-study characteristics. For each scenario, we simulated 500 data sets and fitted both models to each data set. For the initial occupancy probability, the colonization probability, and the extinction probability in both models in each scenario, we calculated the relative bias and mean squared error (MSE).

Eurasian Lynx Case Study

After its total eradication in the Alps by around 1930, the Eurasian lynx (*Lynx lynx*) has been reintroduced multiple times since 1970 in Switzerland, Italy, Austria, and Slovenia (Molinari-Jobin et al. 2018). In the 1990s, experts from the 7 Alpine countries set up the international lynx monitoring program (Status and Conservation of the Alpine Lynx Population). To ensure coverage of its entire territory, the monitoring of the elusive lynx relies on >1300 trained experts (official game wardens and forest service personnel) in 7 Alpine countries. Hunters, naturalists, and other citizens also may be part of the monitoring network. Professional network members search actively for signs and check signs that are reported to them by citizens. We classified signs of presence into 3 reliability categories: C1, hard facts (e.g., dead lynx, lynx removed from the wild as a young orphan and put into captivity, lynx photos, and genetic samples); C2, detections confirmed by a lynx expert (livestock killed by lynx, wild prey remains, and tracks); and C3, data that could not be verified by experts (unverified tracks and wild prey remains) and unverifiable data (e.g., sighting, scat, and vocalization). We treated C1 and C2 data as unambiguous detections, assuming there were no false-positive

Table 1. Parameter values for the 4 simulation scenarios in which parameters controlling the total amount of false-positive and true detections varied.

Scenarios	Initial occupancy probability (ψ_1)	Colonization probability (γ)	Probability of classifying a true detection as unambiguous (b)	False-positive detection probability (p_{10})
High occupancy high *b* (HH)	0.8	0.4	0.8	0.01
				0.5
				0.10
				0.15
				0.20
				0.25
				0.30
High occupancy low *b* (HL)	0.8	0.4	0.5	0.01
				0.5
				0.10
				0.15
				0.20
				0.25
				0.30
Low occupancy high *b* (LH)	0.1	0.1	0.8	0.01
				0.5
				0.10
				0.15
				0.20
				0.25
				0.30
Low occupancy low *b* (LL)	0.1	0.1	0.5	0.01
				0.5
				0.10
				0.15
				0.20
				0.25
				0.30

detections in these data, and C3 data as ambiguous detections. From 1995 to 2014, 8415 observations (67%) were classified as unambiguous detections and 3991 (33%) as ambiguous. If unambiguous and ambiguous detections occurred at a site, we accounted for the unambiguous detections only. Nondetections were obtained on sites that were sampled but where no lynx presence was reported during a survey within a year. Molinari-Jobin et al. (2018) fitted a dynamic occupancy model with unambiguous detections only (i.e., they used our model MU) to assess the effects of environmental covariates on different parameters of the model and to assess distribution-based population trends. A 10 × 10 km grid was used to define the distribution units that corresponded to the approximate home range size of a female lynx in the Alps (Molinari-Jobin et al. 2018). Surveys were defined as 3 replicated 2-month periods: November–December, January–February, and March–April. We used the same data set as Molinari-Jobin et al. (2018), but we added the C3 data and fitted a dynamic occupancy model that combined both unambiguous and ambiguous detections

(MUA). We used the same covariates for the parameters that were common to the models MU and MUA. We considered the effects of forest cover and distance to the release site on ψ_1; the effects of year, forest cover, and number of observed occupied contiguous neighbors on ε; and the same effects plus that of human density and elevation on γ.

For the new parameters in MUA, p_{11} and p_{10}, we used the effect of elevation and forest cover and a random site-by-winter effect to accommodate unmodeled spatial heterogeneity in detection rates in every combination of site and winter. A network covariate was also included to account for heterogeneity in sampling effort in time and space. This covariate took the following values based on the amount of effort for the location and time period: 0, no information available regarding the sampling effort, in which case we assumed it was small but never null because of the presence of at least game wardens and forest service agents who have not been trained in the recognition of lynx signs but report suspect cases (Molinari-Jobin et al. 2012); 1, presence of trained members of the

lynx monitoring network on the site; and 2, members of the lynx monitoring network actively searching for lynx signs. We also considered a linear year effect (i.e., an annual trend) on p_{10} to investigate whether this probability decreased as observers gained experience over time. Finally, we kept the probability b to classify a true positive detection as an unambiguous constant. We considered the effect of a covariate significant if its 95% credible interval (CRI) did not overlap 0.

To evaluate the added value of incorporating the C3 data (ambiguous detections) into the analysis, we compared the maps of occupancy produced by the 2 models by calculating and mapping the difference in the site- and year-specific estimates of realized occurrence $\hat{z}_{i,t}$ (MU) – $\hat{z}_{i,t}$ (MUA).

Codes to run the simulations and fit the models described above are in Supporting Information.

Results

Simulations

For MSE, MUA performed better than MU in all 4 scenarios when $p_{10} \leq 0.15$ (Supporting Information). Above this value both models performed equally well except in 1 scenario and for 1 parameter when estimating the ecological parameters: MUA estimated the colonization probability γ less precisely than MU only in the HL scenario for values of p_{10} between 0.20 and 0.30. The MSE was highest (range 0.04–0.25) in the HL scenario and ranged from 0.04 to 0.14 in the HH scenario. The MSE was lowest in the LH scenario and ranged from 0.02 to 0.06 and 0.02 to 0.11 in the LL scenario.

Both models estimated ψ_1 and γ with biases below or equal to 5% in the HH, HL, and LH scenarios (Supporting Information). In the LL scenario, MU estimated ψ_1 with a bias above 5% (up to 8%) and MUA had a lower bias than MU. For ε, MUA performed better or equivalently above 5% in terms of bias in the scenarios HH and HL and worse or equivalently above 5% in the LH and LL scenarios.

Lynx Case Study

When we fitted the MUA with both unambiguous and ambiguous detections (i.e., for C1, C2, and C3 data), p_{11} was higher on sites with a high forest cover and appeared to vary according to the season and network (Table 2). Elevation had no effect on p_{11}. The p_{10} was higher on sites with a high forest cover and varied according to network (Table 2). Although elevation and season had no significant effect on p_{10}, this probability decreased over time (Table 2). Both models gave similar estimates for ψ_1, ε, and γ, but MUA produced more precise estimates than MU (Supporting Information).

The b was estimated at 0.81 with high precision (CRI 0.79–0.83). At the beginning of the study period, in the winter 1995 and 1996, we estimated the mean ψ over all sites at 0.04 (CRI 0.03–0.07), p_{11} at 0.11 (CRI 0.10–0.25), and p_{10} at 0.006 (CRI 0.004–0.01). For the end of the study period, winter 2013 and 2014, we estimated the mean ψ at 0.1 (CRI 0.0899–0.11), p_{11} at 0.17 (CRI 0.09–0.24), and p_{10} at 0.007 (CRI 0.003–0.010). MUA estimated a few more occupied sites than MU for both winters 1995 and 1996 and 2013 and 2014 (4 [1995 and 1996] to 13 [2013 and 2014]) (Fig. 1) and estimated occupied sites that were estimated occupied by MU too. The additional sites that were estimated occupied from MUA were sites where ambiguous detections occurred (Fig. 1).

Discussion

Assessing the distribution of large carnivores at large scales is vital information for assessing their conservation status and abundance (IUCN 2012; Jedrzejewski et al. 2018), identifying potential conflict areas (Marucco & Mcintire 2010), and, for successful management, understanding the mechanism behind distribution dynamics (Eriksson & Dalerum 2018). Producing more precise and less biased estimates by adding ambiguous data with a model accounting for false-positive detections can bring new insights to the distribution of species where getting unambiguous data is challenging. Due to the large areas involved, the monitoring of large carnivores in Europe relies on a large network of both professional and nonprofessional observers (Louvrier et al. 2018; Molinari-Jobin et al. 2018). Although false-negative detections have received much attention in the literature of species distribution modeling with the rise of occupancy models (MacKenzie et al. 2003; Bailey et al. 2014), dealing with ambiguous detections has been studied much less (Miller et al. 2011; Chambert et al. 2015). Here, our simulations demonstrated that jointly analyzing unambiguous and ambiguous detections with the appropriate dynamic occupancy models can lead to increased precision in the estimates of ecological parameters when p_{10} is low. When this probability was >0.20, both models estimated ecological parameters with almost equivalent precision, which varied between its highest values in the high occupancy scenarios and its lowest values in the low occupancy scenarios. Both models produced estimates of ecological parameters with low bias except for one ecological parameter in one specific scenario. When looking at the results of the lynx analysis, adding ambiguous data helped produce more precise estimates and provided additional spatial information that improved inference in areas where the species likely occurred at very low density (e.g., at a colonization front).

Table 2. Parameters estimates for the detection probabilities from the dynamic occupancy model accounting for unambiguous data only and accounting for unambiguous and ambiguous data. Both models were fitted on Alpine lynx data from 1995 to 2014.[a]

	Model with unambiguous data only (MU) Detection probability (p)				Model with ambiguous and unambiguous data only (MUA) True detection probability (p_{11})				Model with ambiguous and unambiguous data only (MUA) False-positive detection probability (p_{10})			
	mean	SD	x	y	mean	SD	x	y	mean	SD	x	y
Intercept	−3.88	0.46	−4.88	−3.04	−3.14	0.47	−4.15	−2.33	−5.37	0.29	−5.96	−4.80
Effect of elevation	−0.11[b]	0.05[b]	−0.20[b]	−0.01[b]	−0.07	0.04	−0.16	0.01	−0.02	0.06	−0.13	0.09
Effect of forest	0.63[b]	0.07[b]	0.50[b]	0.75[b]	0.67[b]	0.06[b]	0.55[b]	0.79[b]	0.37[b]	0.06[b]	0.26[b]	0.49[b]
Effect of season 2	0.26[b]	0.07[b]	0.12[b]	0.40[b]	0.22[b]	0.07[b]	0.08[b]	0.35[b]	−0.14	0.12	−0.38	0.09
Effect of season 3	0.42[b]	0.07[b]	0.28[b]	0.57[b]	0.42[b]	0.07[b]	0.29[b]	0.56[b]	−0.04	0.12	−0.25	0.19
Effect of network 1	1.21[b]	0.21[b]	0.77[b]	1.60[b]	0.92[b]	0.20[b]	0.54[b]	1.31[b]	0.37[b]	0.14[b]	0.09[b]	0.66[b]
Effect of network 2	2.37[b]	0.23[b]	1.93[b]	2.84[b]	1.95[b]	0.22[b]	1.53[b]	2.40[b]	2.63[b]	0.30[b]	2.02[b]	3.20[b]
Residual effect	0.86	0.10	0.65	1.04	0.90	0.06	0.77	1.01	0.42	0.21	0.18	0.92
Effect of country France	−3.49[b]	0.31[b]	−4.09[b]	−2.87[b]	−2.76[b]	0.28[b]	−3.32[b]	−2.21[b]	−5.55[b]	0.25[b]	−6.05[b]	−5.06[b]
Effect of country Italy	−3.40[b]	0.24[b]	−3.86[b]	−2.94[b]	−2.85[b]	0.23[b]	−3.31[b]	−2.40[b]	−5.55[b]	0.24[b]	−6.01[b]	−5.07[b]
Effect of country Switzerland	−2.87[b]	0.23[b]	−3.32[b]	−2.42[b]	−2.23[b]	0.22[b]	−2.68[b]	−1.81[b]	−4.75[b]	0.26[b]	−5.25[b]	−4.25[b]
Effect of country Austria	−4.00[b]	0.25[b]	−4.48[b]	−3.51[b]	−3.25[b]	0.21[b]	−3.67[b]	−2.84[b]	−5.62[b]	0.23[b]	−6.07[b]	−5.16[b]
Effect of country Slovenia	−4.54[b]	0.35[b]	−5.23[b]	−3.86[b]	−3.83[b]	0.34[b]	−4.51[b]	−3.19[b]	−4.62[b]	0.28[b]	−5.17[b]	−4.05[b]
Effect of country Germany	−4.99[b]	1.39[b]	−8.28[b]	−2.65[b]	−3.93[b]	1.52[b]	−7.41[b]	−1.51[b]	−6.11[b]	0.49[b]	−7.21[b]	−5.23[b]
Effect of time in years	-	-	-	-	-	-	-	-	−0.04[b]	0.02[b]	−0.09[b]	−0.01[b]

[a]Both models were fitted on Alpine lynx data collected from 1995 to 2014. Means are posterior means; x and y are lower and upper bounds of the 95% Bayesian CI.
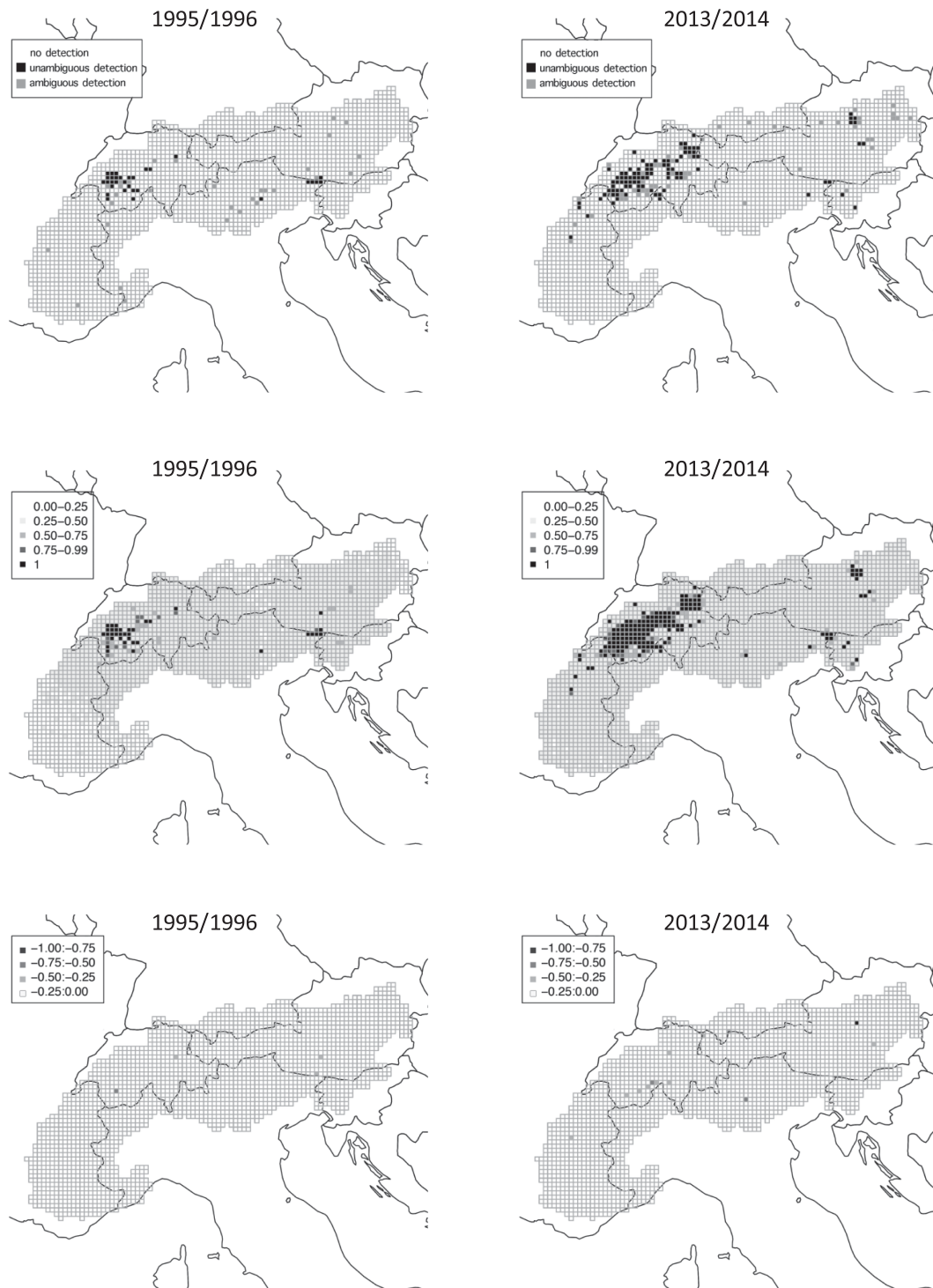[b]Effects with 95% Bayesian CI that do not contain zero.

Figure 1. *(Top row) Locations of Lynx observation (i.e., raw data) in the winters of 1994 and 1995 and 2013 and 2014 (black sites, unambiguous detections occurred; gray sites, ambiguous detections occurred); (middle row) estimated lynx distribution (probability of occurrence 0–1) in the Alps in the winters of 1994 and 1995 and 2013 and 2014 for the model with ambiguous data (not used on figure) (black sites, sites with a probability of occupancy of 1; white sites, sites with a probability of occupancy of 0); (bottom row) and mapped differences in occupancy estimates between the model with unambiguous data only (value on the right in key) and the model with unambiguous and ambiguous data for the winters 1994 and 1995 (left) and 2013 and 2014 (right) (value on left) (gray sites, model with ambiguous data predicted a higher occupancy probability than the model with unambiguous data only).*

Simulation Lessons

MUA performed better than MU in most of the scenarios. Two factors seemed to have an influence on models' performances: the false-positive probability and the occupancy probability. In terms of precision, MUA performed better when p_{10} was low and performed equivalently when p_{10} was high. In the case of a low occupancy probability, the estimates of extinction probability were more biased positively under the MUA than the MU, leading to an overestimation of ε and the distribution. For the other parameters and the other scenarios, MUA produced estimates with low biases. Whether a species occurs at high or low occupancy probability can often be evaluated prior to the analyses based on the knowledge of the species ecology or on previous studies. We recommend always including ambiguous data because in most of the scenarios MUA performed better than or equivalently to MU in terms of both precision and bias for the ecological parameter estimates.

Accounting for Ambiguous Data When Studying Distribution of Large Carnivores

Our SDM exercise with lynx allowed assessment of trends in the distribution of the species, and these trends can be used to inform their conservation status (Guisan & Thuiller 2005). Our covariate effects were similar in direction and magnitude to those estimated by Molinari-Jobin et al. (2018), who fitted the simpler MU to the lynx data with unambiguous detections only (Table 2). (See Molinari-Jobin et al. [2018] for a detailed description of these effects and their possible biological interpretation.) Our results showed that the probability of a false-positive detection decreased over time. This could be due to observers remaining in the network becoming less likely to make false-positive detections over time as they became more experienced in recognizing the species (Jordan et al. 2012). This was corroborated by the fact that the number of ambiguous detections decreased over the study period (Molinari-Jobin et al. 2012). Additionally, the use of camera trapping has increased over time and has led to an increased number of C1 detections and therefore diminished the proportion of C3 in the data sets (Molinari-Jobin et al. 2018). The learning process of citizens in scientific monitoring programs has been studied (Dickinson et al. 2012; Jordan et al. 2012). The general public not only learns through participation, but also becomes more aware of the general ecological issues and more prone to understand scientific research (Bonney et al. 2009). We found that the probability of making a true detection was similar to the probability of detecting the species in MU fitted by Molinari-Jobin et al. (2018). This makes sense because the probability of detecting the species in MU was equal to the probability of making a true detection multiplied by the probability

of classifying a detection as unambiguous. We also found that there was a probability of 0.8 of classifying a true detection as unambiguous. This may be due to the fact that observers in the network were highly competent at detecting the species and producing reliable data. This finding may also reflect that it is relatively easy to identify the signs of presence of lynx because there is almost no confusion possible with other species present in the area. Whenever the focus species can be mistaken for another species, if the quality of data is not sufficient (e.g., dog tracks in the snow mistaken for wolf tracks), true detections can be classified as ambiguous. There can also be false-positive detections from misidentification when b is low. In this case, the amount of true detections in ambiguous data will not be negligible. In a case where b is low and only unambiguous data are used, a large part of true presences can be missed and the resulting distribution will be underestimated (Miller et al. 2011).

The occupancy estimates under both models suggest the lynx case study corresponds to the LH simulation scenario (compare Table 1 with Supporting Information). For the distribution maps produced by MUA, adding ambiguous detections brought new and useful information. Some sites were estimated as occupied by MUA, whereas these same sites were estimated as unoccupied by MU (Fig. 1). Because of the low occupancy of the lynx and its elusive behavior, the number of times the species was detected was very low. Because the probability to classify a detection as unambiguous b was high, only a few true detections were classified as ambiguous, which may explain why adding them did not change the parameter estimates but helped produced more precise estimates. In turn, adding ambiguous detections provided new insights related to management of a protected species (Guillera-Arroita et al. 2015). The sites we found to be occupied because of the incorporation of ambiguous detections could likely represent areas where the species is currently expanding. These same sites also may be places where lynx have not occurred before and negative interactions may occur due to the novelty of lynx presence. Sites that appeared occupied after including ambiguous data can inform the prediction of location of potential conflicts. Finally, if the objective is to map the colonization front to, for example, mitigate conflicts, ambiguous data should be included.

Recommendations

Dynamic occupancy models in general provide a powerful and natural analytical framework for changing species distributions (Kéry et al. 2013). More specifically, dynamic occupancy models accounting for misidentification represent a powerful method to deal with detections that cannot be categorized as certain in species distribution modeling. We recommend careful categorization of field observations into unambiguous or ambiguous

detections, for instance by using several experts to classify the detections and a standardized filtering classification process to avoid false-positive detections mistakenly classified as reliable data. This filtering process also allows rejecting detections that can be identified easily as false positives. If some detections cannot be checked by experts for instance and cannot be classified as unambiguous, observers may need to visit the sites where these detections were made to get more reliable detections. Even though occupancy models can deal with ambiguity, survey should be designed and data collected so as to avoid the production of false-positive detections or at least reduce their proportion. In the case of data from CS projects, models accounting for false-positive detections are a relevant tool to assess species distribution if a classification of detections is made (e.g., unambiguous vs. ambiguous). In the case of a species occurring at low density, such as the Eurasian lynx, additional information can provide new insights into the species distribution and help target specific sites where the species is likely to occur in the future.

Acknowledgment

Supporting Information

The scripts used for running the simulations (Appendix S1) and to fit our model to the lynx data (Appendix S2), the resulting biases and MSE from 4 scenarios of the simulation study (Appendix S3), and the estimates of ecological parameters in the MU and MUA models (Appendix 4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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