On the effects of grid size and shape when mapping the distribution range of a recolonising wolf (*Canis lupus*) population

Eric Marboutin · Marie Pruszek · Clément Calenge · Christophe Duchamp

Abstract An estimate of changes in a species' distribution range is a key variable in assessing its conservation status. It may be based on the direct detection of individuals, or on the use of indirect presence sign surveys. In both cases, the process requires one to switch from a point-based approach, where individuals/presence signs are located using a coordinate system, to an area-based one, each original point being replaced by a cell area unit (CAU), with a given shape and size. The estimated distribution range (EDR) is the spatial union of the CAUs over the area of interest. Based on wolf presence signs collected in France (1996–2006), we analysed the influence of the shape and size of types of CAUs (circular area versus square grid mesh; 6, 25, 50 and 100 km^2) on the changes in EDR. EDR increased with time and a saturating phase was noticed by the end of the period. We assessed the effects of the year and the type of CAU on EDR using exploratory data analysis. Larger CAUs resulted logically in larger EDR values, whatever the CAU shape. For a given CAU size, contiguous square grids yielded larger EDR values than overlapping circular buffers. The effect of the interactions between the year and the type of CAU on EDR changes was evidenced using an auto-modelling method based on principal component analysis. Compared to smaller units, larger CAUs resulted in larger growth rates during the range increase phase, and in smaller rates during the saturating phase. A basic and descriptive conceptual model helped interpreting this pattern as a consequence of the characteristics of the colonisation process in the wolf population. We discuss the present results within the framework of conservation status assessment and management of the wolf population.

Keywords Distribution area · Index · Trend · Exploratory data analysis · Wolf · France

E. Marboutin (✉) · M. Pruszek
Oncfs,
ZI Mayencin,
38610 Gières, France
e-mail: eric.marboutin@oncfs.gouv.fr

M. Pruszek
e-mail: marie.pruszek@club-internet.fr

C. Calenge
Oncfs,
Saint-Benoist,
78612 Le Perray-en-Yvelines, France
e-mail: clement.calenge@oncfs.gouv.fr

C. Duchamp
Oncfs,
Micropolis La Bérardie,
05000 Gap, France
e-mail: christophe.duchamp@oncfs.gouv.fr

Introduction

Assessing the conservation status of any species requires information about several parameters, in particular the distribution range of the population. However, for some elusive or rare species such as large carnivores, the direct detection of individuals is usually unfeasible: the distribution range of the population would be better inferred from indirect monitoring, such as presence sign surveys (Linnell et al. 1998; Kunkel et al. 2005). Indeed, the presence signs, including foot prints, preys, scats, etc., can be more easily collected and mapped. These presence data define a spatial point-pattern, as would do data inferred from the direct monitoring of animals (e.g. based on telemetry). A central question is then how to estimate the distribution area of the

focus species from its locations: how does one switch from a zero-dimensional process (points) to a two-dimensional process (surface)? Different approaches have been developed: some of them focus on the modelling of the extent of occurrence (e.g. Pearce and Boyce 2006), others rely on the estimation of the area of occupancy (e.g. Telfer et al. 2002). In both cases, the algorithms used may interfere with conservation issues (e.g. Araujo and Williams 2000; Araujo 2004), like for other components of population status assessment (e.g. Patterson and Murray 2008).

Since the actual size and shape of the distribution range is usually unknown, only a relative picture can be inferred from the field data, and compared over time. An intuitive representation of this distribution range consists in associating to each presence sign a cell area unit (CAU) with an ad hoc size and shape (buffer, grid quadrat, etc.) (IUCN 2008); the estimated distribution range (EDR) of the population is then measured by the union of all the CAUs in which presence signs were detected. The size of the EDR is therefore an obvious function of the size of the CAU (the larger the latter, the larger the former; IUCN 2008, p. 35), but also possibly of the shape of the CAU (e.g. an overlapping circular CAU may yield more conservative estimates than a non-overlapping square grid CAU). This raises the question of the influence of the CAU size and shape on the resulting estimates of changes in the EDR, and therefore on the perception of biological processes occurring at this scale (Thomas and Abery 1995).

We address this question in this paper using a case study of the wolf population in France that is currently expanding (Cubaynes et al. 2009). The E.C. Habitats Committee has adopted a standardised reporting format for the assessment of species' conservation status under article 17 of the Directive 92/43 (E.C. 2006). Emphasis is given on using standardised mapping procedures and grids, so that data from neighbouring countries can be further pooled to build up common detection/non-detection maps. The European Environmental Agency provides a 10×10-km cell grid (EEA; http://data service.eea.europa.eu/dataservice/metadetails.asp?id=760), which should be used for this report. What are the consequences of choosing a 100 km² CAU to estimate the EDR on the perception of the biological processes occurring at the scale of a species' distribution range? What would be the effect of a different choice of CAU shape and size on the EDR and its time-related changes?

In the present paper, we compare changes in the EDR of the French wolf population over an 11-year period, using two shapes for the CAU (circular, square) and four sizes ranging from 6 to 100 km². The largest CAU, we used (100 km²) was still a conservative approach to home range size in wolves (Mech and Boitani 2003), whereas the smallest one (6 km²) was close to default values recommended by IUCN (2008, p. 33).

Material and methods

Wolf data

This population is monitored since 1994 based on a network involving 882 trained field experts who collect presence signs all year long (following Linnell et al. 1998) and on non-invasive genetic monitoring (Valière et al. 2003). During the study period (1996–2006), more than 10,000 presence signs were validated and used for further analysis, including non-invasive genetic sampling (scats, urine, hair, blood; $n=1,160$ wolf positive), wild and domestic preys, prints, sightings and photos and howlings. For each presence sign detected, a standardised form was filled with all the technical criteria needed for further analysis (e.g. description of bites and consumption of preys; path and tracks measurements and alignment for snow-tracking data; etc.). We classified data as uncheckable if only less than half of the criteria were described, or checkable and wolf related if all of the criteria pointed at wolf characteristics. As soon as one criterion did not match with expectations from an actual wolf sign, the sign was discarded (e.g. wrong tail length). By late 2006, the wolf population was made of 17 packs, including five trans-boundary ones. This French population segment is part of the Alpine population that is shared between Switzerland, Italy, and France (Linnell et al. 2007).

GIS mapping

Point data were georeferenced to the extended Lambert II projection and mapped using Arcview 9.2 (Esri 2007). For each year, nine maps were computed based on four CAU sizes (6, 25, 50 and 100 km²) and two geometric shapes (circular buffers around each observation and quadrat grids centred over France). We also used the 10×10-km grid from EEA, centred over Europe. Overall, nine EDR values per year were calculated. Circular CAUs could overlap whereas those from the grid quadrats were contiguous (Fig. 1).

Data analysis

We performed an exploratory analysis of the dataset to identify the effect of the CAU size and shape on the EDR, using graphical methods, as recommended by Tukey (1977) and more recently by Cleveland (1993). We chose an exploratory approach because: (a) we had no a priori idea of the possible models able to correctly describe the complex biological processes underlying wolf colonisation in France and (b) it is likely that the common assumptions underlying classical inferential methods are violated (independence between sampling units, known distribution, etc.).
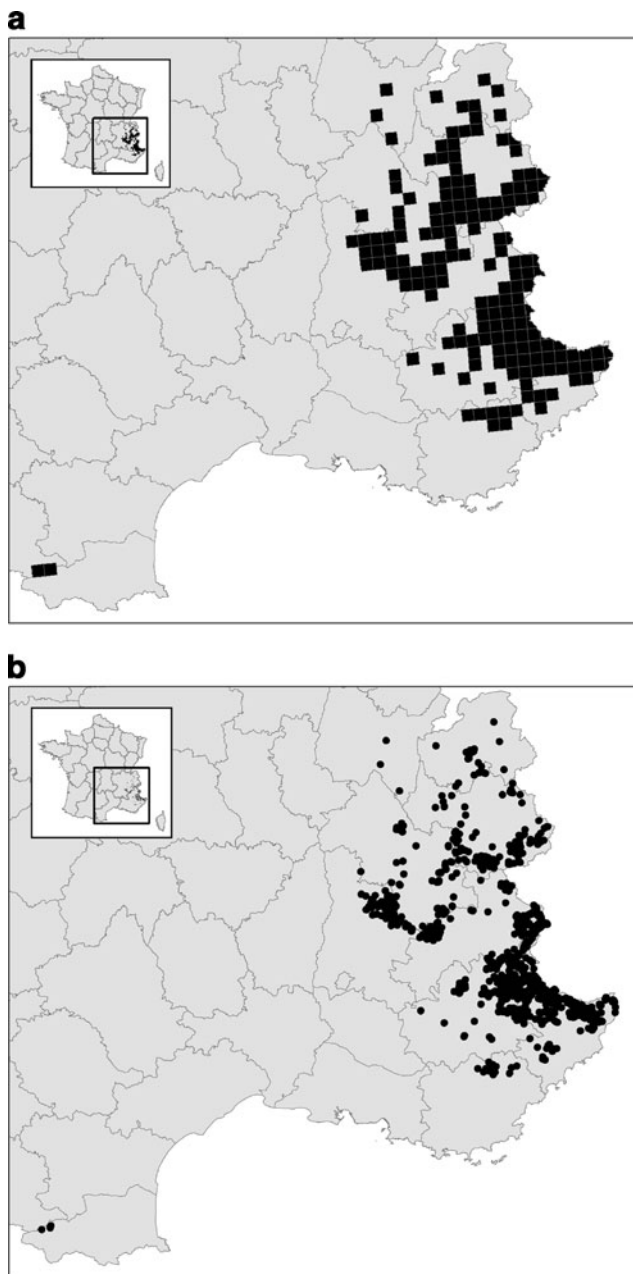
a

b

Fig. 1 Example of the estimated wolf distribution range in 2005, based either on a 10×10 km grid mesh (**a**) of contiguous quadrats or on 25 km^2 circular and overlapping buffers (**b**)

We first identified the main characteristics of the wolf expansion in the French Alps, by looking at the temporal changes of the EDR once averaged over CAU types: first, one value was calculated per year and per CAU shape and size; second, the resulting nine EDRs were averaged within each year and third, the averaged EDRs were plotted as a function of time ($n=11$ years). We then calculated the residuals of this simple graphical model to study the differences between the EDR estimated using the different CAU shapes and sizes and the averaged EDR for each year. This allowed us to identify the effects of the type of CAU

on the EDR. Basically, we thus fitted a simple model predicting the EDR according to the additive effects of the year and the type of CAU.

Finally, we studied the residuals of this additive model to identify a possible effect of the interactions between the type of CAU and the year on the EDR. We used the principal component analysis (PCA) as an auto-modelling method (Chessel and Thioulouse 1991) for studying these interactions. We briefly describe this method here. Let **X** be the table containing the value of the EDR for a given type of CAU (column) for a given year (row). This table is centred by row (the mean of the EDR for each year is equal to 0) and by column (the mean of the EDR for each type of CAU is equal to zero). Consequently, this table contains the residuals of the additive model described above. The principal component analysis of this table consists in the diagonalisation of the matrix **V**:

$$\mathbf{V} = \mathbf{X}^t \mathbf{X}/n$$

Where $\mathbf{X}^t$ denotes the transpose of **X**, and n is the number of years in the study (here equal to 11). This diagonalisation returns a set of vectors $\mathbf{u}_i$ containing the scores of the types of CAU on the principal axes, a set of vectors $\mathbf{v}_i$ containing the scores of the years on the principal components and a set of eigenvalues λ_i measuring the variance of the scores on the principal components/axes (in the special case of a PCA performed on a table centred by row and by column, the variances of the scores of the rows on a given principal component is identical to the variance of the scores of the columns on the corresponding principal axis). Let $\mathbf{u}_i^* = \mathbf{u}_i/\sqrt{\lambda_i}$ and $\mathbf{v}_i^* = \mathbf{v}_i/\sqrt{\lambda_i}$ be the eigenvectors containing the normed scores of the types of CAU and years on the ith principal component (i.e. the scores scaled such that their variance is equal to 1). A well-known property of the PCA (Gabriel 1971) is that:

$$\mathbf{X} = \sum_i \mathbf{v}_i^* \mathbf{u}_i^{*t} \sqrt{\lambda_i}$$

The value of the EDR for a given year and a given type of CAU is equal to the sum over all principal components of the normed score of the type of CAU multiplied by the score of the year. It is therefore possible to "reconstitute" the table **X** using only a restricted set of principal components. In this study, we used only the first principal component for this auto-modelling operation (see "Results") so the interaction between the year and the type of CAU is considered to be of the form: $\alpha_k \cdot \beta_l$, where α_k is the effect of the CAU k and β_l is the effect of the year l. All analyses were conducted using R software (R Development Core Team 2008).

The scale dependence in the yearly growth of log$_2$-transformed EDR was further quantified from the extreme

CAU sizes (100 km^2 versus 6 km^2). We computed the sum of squares of discrepancies in EDR growth as a function of scale over the study period, and compared it between grids and buffers using:

$$\sum_{t=1}^{t=11}\left[\left(2^{\log(EDR_{t+1})-\log(EDR_t)}\right)_{\text{quadrats100}} - \left(2^{\log(EDR_{t+1})-\log(EDR_t)}\right)_{\text{quadrats6}}\right]^2,$$

on one hand for S.S.D.$_{\text{quadrats}}$ and

$$\sum_{t=1}^{t=11}\left[\left(2^{\log(EDR_{t+1})-\log(EDR_t)}\right)_{\text{buffers100}} - \left(2^{\log(EDR_{t+1})-\log(EDR_t)}\right)_{\text{buffers6}}\right]^2,$$

on the other hand for S.S.D.$_{\text{buffers}}$

Results

First data visualisation

We noticed a strong and positive effect of CAU size on the EDR, and the dispersion between curves increases with increasing EDR (Fig. 2a). This suggests a multiplicative growth (Cleveland 1993): the area newly colonised by wolves during year t is proportional to the area estimated during year $t-1$. The larger the EDR_{t-1}, the larger the EDR_t. When using log$_2$-transformed data, the curves are parallel (Fig. 2b) and the difference between two consecutive EDR values must be regarded as a relative growth $[\log(EDR_{t+1}) - \log(EDR_t) = \log(EDR_{t+1}/EDR_t)]$. For example, with a quadrat CAU covering 6 km^2, $\log(EDR_{1996}) = 8.5$ and $\log(EDR_{2006}) = 11.5$. The difference is 3, so during the 11-year period, the EDR increased with a 2^3 factor, i.e. $EDR_{2006} = 8 \times EDR_{1996}$; due to an apparent strong parallelism between curves, this result might seem at first glance weakly dependent on the shape and size of the CAU (contrary to absolute growth that could be inferred from non-log-transformed data). The EDR however increased sharply in the beginning of the study period, then a saturating phase was noticed by the end. One may question therefore about the constancy of parallelism over these phases (increase, saturation), as a function of CAU shapes and sizes.

Graphical data modelling

The visual analysis of Fig. 2b suggests an additive model where log(EDR) is a function of YEAR and CAU. When calculated by year and for a given CAU size, the difference $\log(EDR_{\text{quadrats}}) - \log(EDR_{\text{buffers}})$ was most often positive (43 instances out of 55 possible values) but larger early in the study period than later on. This possible interaction between YEAR and the type of CAU was further evidenced by means of a PCA applied to log(EDR) once the table was centred by row and columns (see "Data analysis")

The eigenvalue of the first axis was four times as large as any other, so we focused only on the first axis for the auto-modelling process (Fig. 3c). This operation allowed us to identify visually the main patterns occurring in the residuals of the model predicting the EDR as an additive effect of the year and the type of CAU (Fig. 3a and b).

The size of the CAU, rather than its shape, appeared to be the main cause of the pattern modelled by the PCA on its first axis, and this pattern discriminated markedly 3 years as opposed to the rest of the period (Fig. 3b). Early in the period, larger CAUs tended to produce EDRs larger than those expected under the hypothesis of additivity of the effects of the year and the type CAU. Later on (from 2000 onwards), smaller CAUs tended to produce EDRs larger than those expected under this hypothesis of additivity (Fig. 3b).

The pattern in log$_2$(EDR) as a function of either cell area or time is however much stronger than that coming from their interaction (Fig. 4): the variation in the response variable was about ten times less in the latter than in the former.

Fig. 2 Time-dependent changes in the estimated wolf distribution range in France (*EDR*) as a function of cell area unit shape (quadrats or buffer) and size (6, 25, 50 and 100 km^2): **a** changes in EDR on a linear scale; **b** change in EDR on a logarithmic scale (base 2 was chosen for this logarithm)
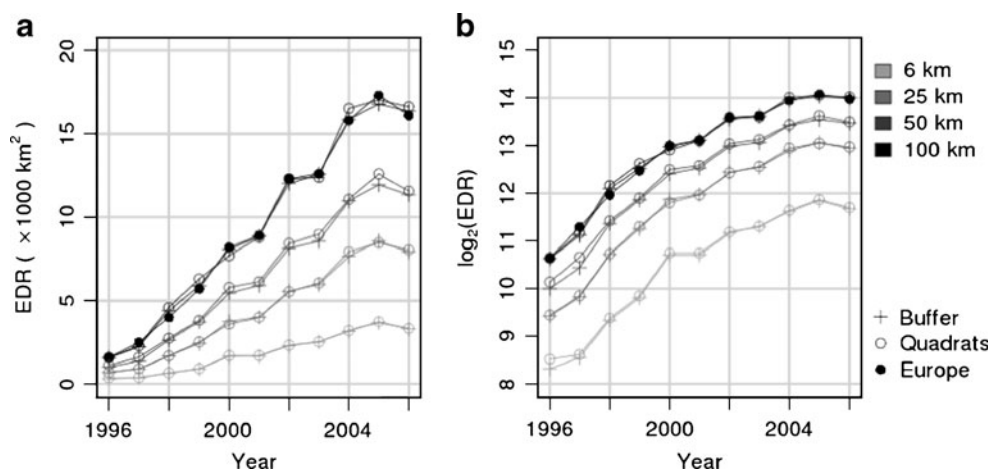
Fig. 3 a Time-dependent changes in the residuals of the additive model predicting the estimated distribution range of the wolf in France as a function of the type of cell area unit used and year; **b** auto-modelling of these residuals using the first axis of a principal component analysis (*PCA*) of the table containing these residuals; **c** *Barplot* showing the eigenvalues of this principal component analysis
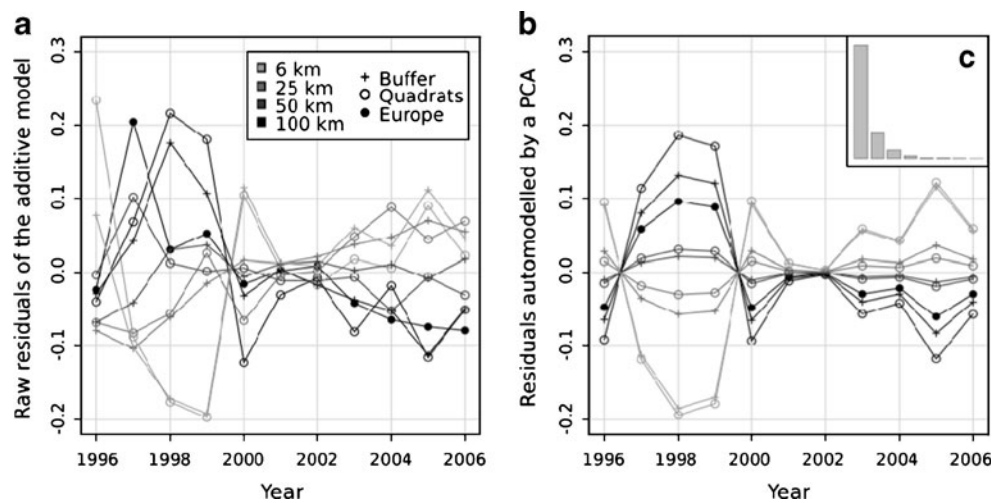
EDR growth patterns

Figure 4 suggests that (a) changes in EDR were greater before 2000 than after (Fig. 4a) and (b) compared to small CAUs, larger ones emphasised this pattern in the data: the strong growth phase was accentuated, whereas the saturating one was smoothed.

Fig. 4 Summary of the model fitted to explain the estimated distribution range (*EDR*). On each figure, a *grey rectangle* with fixed size indicates the importance of each identified pattern: **a** year effect expressed as the mean deviations for each year from the mean EDR over all years and all types of cell area units; **b** cell area unit effect, expressed as the mean deviation for each type of CAU from the mean EDR cover all years and all types of CAU (*B* buffer, *Q* quadrats; the number indicates the area of the CAU in km²); **c** auto modelling by a principal component analysis (*PCA*) of the interactions between the year and the type of CAU; **d** residuals of this model

When such discrepancies are observed conditional on size or shape of the CAU, one is bound to provide the largest [min, max] interval for changes in the EDR (Table 1), rather than arbitrarily choosing one of the point estimates. For example, the expansion of the EDR between 1996 and 1997 should be considered in the range $\left[2^{\log(EDR1997)-\log(EDR1996)}\right]_{quadrats6}$ to $\left[2^{\log(EDR1997)-\log(EDR1996)}\right]_{quadrats100} = [1.06, 1.44]$, or
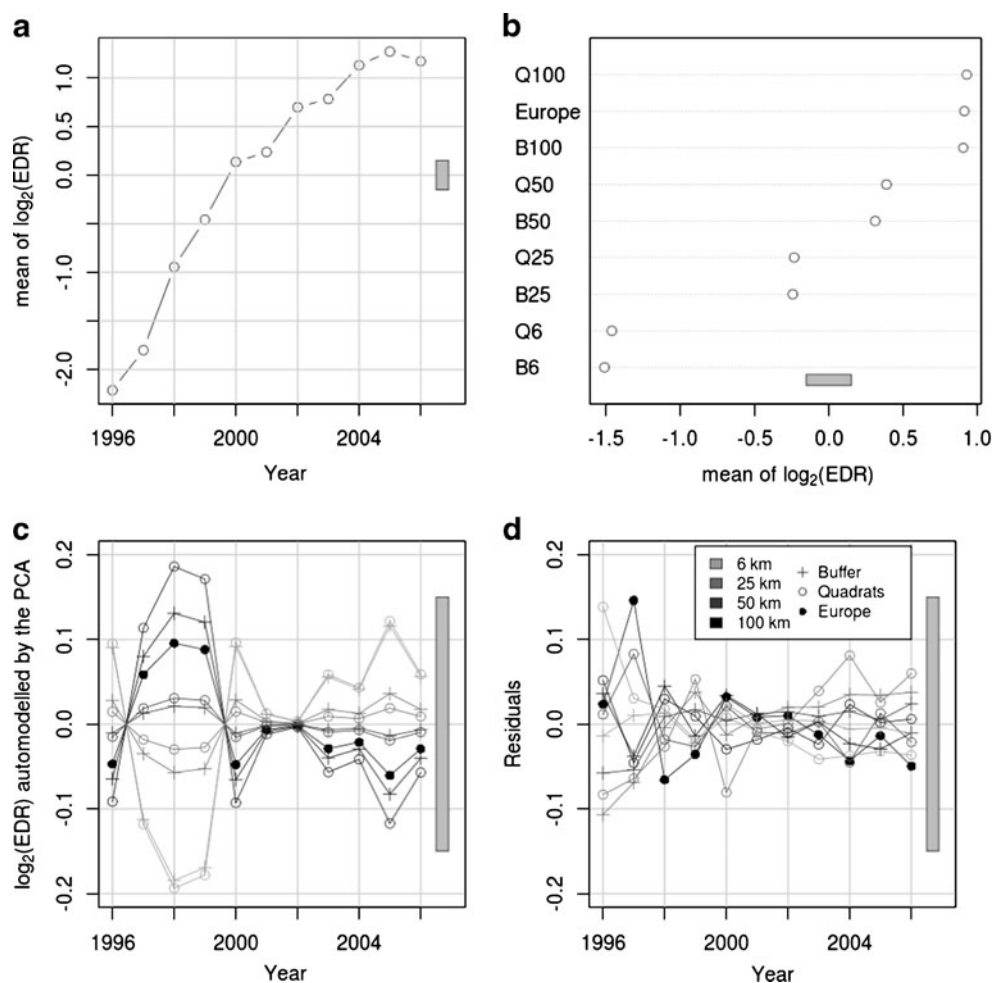
Table 1 Yearly changes in estimated distribution range (EDR) as a function of cell area unit (CAU) shape (contiguous quadrat grids, overlapping circular buffers) and utmost sizes (6 km2, 100 km2) based on more than 10,000 wolf presence signs collected from 1996 to 2006 in France

Growth of EDR	Quadrat grids		Circular buffers	
	6 km^2	100 km^2	6 km^2	100 km^2
1996–1997	1.06	1.44	1.18	1.40
1997–1998	1.69	2.00	1.72	1.97
1998–1999	1.39	1.37	1.39	1.34
1999–2000	1.87	1.22	1.87	1.38
2000–2001	1.00	1.14	1.00	1.09
2001–2002	1.36	1.40	1.37	1.36
2002–2003	1.09	1.01	1.10	1.05
2003–2004	1.22	1.33	1.25	1.26
2004–2005	1.21	1.03	1.16	1.06
2005–2006	0.89	0.98	0.90	0.98
	S.S.D.$_{\text{quadrat grids}}$=0.73		S.S.D.$_{\text{circular buffers}}$=0.39	

[1.18, 1.40] if it is estimated from buffers of 6 or 100 km^2. This scale effect on EDR growth was weaker however when using circular buffers than when using grids as evidenced by the sum of squares of differences (S.S.D.$_{\text{buffers}}$=0.39; S.S.D.$_{\text{quadrats}}$=0.73).

The scale effect was also weaker for long-term changes in the EDR (i.e. trends in the species' range), than when focusing on yearly changes, particularly when EDR growth was estimated from circular buffers: $\left[2^{\log(\text{EDR2006})-\log(\text{EDR1996})}\right]_{\text{quadrats6}} = 9$ compared to $\left[2^{\log(\text{EDR2006})-\log(\text{EDR1996})}\right]_{\text{quadrats100}} = 10.4$; $\left[2^{\log(\text{EDR2006})-\log(\text{EDR1996})}\right]_{\text{buffers6}} = 10.3$ compared to $\left[2^{\log(\text{EDR2006})-\log(\text{EDR1996})}\right]_{\text{buffers100}} = 10.4$.

Discussion

Our results stemmed from a descriptive and graphical analysis (sensu Valois 2000). It is important to stress that an exploratory analysis of data will mostly document patterns within them when there are no a priori expectations, contrary to traditional hypothesis testing designed to verify such a priori hypotheses (Tukey 1977). The former does not result into conclusions associated to e.g. a p value, but rather provides working hypotheses concerning the studied processes. Within this framework, data help defining a conceptual model that may likely underlie the observed process.

A conceptual model for the colonisation process

The estimated distribution range increased over time, but two phases could be distinguished, a strong increase phase,

then a saturating phase. Mapping with the largest cell area unit resulted in a larger EDR, which is trivial. Our main working issue was to identify the process underlying the interaction between the type of CAU and year factors. Why do larger CAUs lead to different perceived changes in the EDR compared to smaller ones, depending on the growth phase? A simple model can be proposed, based on the influence of the distance between the already documented presence area and locations of new wolf presence signs. Let us consider a fictive EDR at time t that is estimated from one presence sign, using either square or circular shapes as buffers of e.g. 6 or 100 km^2. At time $t+1$, let another presence sign be found at the same place, together with another one, close to the former (Fig. 5a). The relative
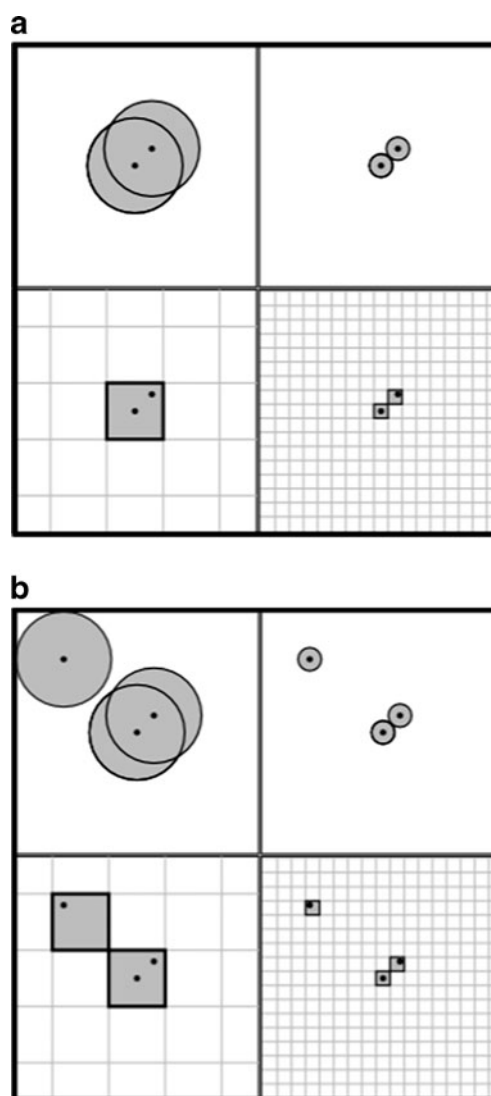

Fig. 5 A simulated spatial growth process (**a** time $t+1$; **b** time $t+2$) that results in different values of changes in the estimated distribution range (grey areas), depending on the shape and size of the cell area unit and on the distance between presence signs (black dots)

growth EDR_{t+1}/EDR_t is 2 with small buffers, and always less than 2 with large buffers as long as their size is large enough compared to the distance between the presence signs. At $t+2$, the two presence signs may still be recorded at the same places, together with a third one, somewhat farther apart (Fig. 5b). Now EDR_{t+2}/EDR_{t+1} is $3/2=1.50$ with small circular CAUs, and $2.36/1.36=1.74$ with large ones. With square grids, the discrepancy may be even larger ($3/2=1.5$ with small cells compared to $2/1=2$ with large ones).

The interaction between the size of the CAU and estimated changes in the EDR may therefore partly be a consequence of how large the distances between already documented presence signs and newly documented ones are, compared to the CAU size and shape. Considering the French wolf population, this means that the slower the colonising process, the stronger the smoothing effect of large CAUs on estimated changes in the EDR. Conversely, when the colonising process is faster (i.e. newly colonised areas are farther from already-known presence areas), small-sized CAUs tend to underestimate changes in the EDR compared to larger ones.

Consequences regarding the population status assessment

The actual range and related changes over time are unknown. No reference value is available for calibrating the mapping system, so we cannot determine which of the different cell area units at hand is the best one in the absolute. One might wish to adjust the process of evaluating changes in the species range based on a time-related scale (short-term fluctuations versus long-term trends) and the status of the population inferred from other indicators, such as population size, threats, etc.

As far as short-term changes in the EDR are concerned (e.g. on a year-to-year basis), it seems more appropriate to use an interval-based presentation of the results using minimum and maximum estimated changes in EDR as a function of CAU size and shape (see "EDR growth patterns"). It would enlight the uncertainty in the results due to the analysis itself, whereas focusing arbitrarily on a given point estimate would be misleading. This form of uncertainty should be implemented in the decision-making process (Bradshaw and Borchers 2000), based preferably on circular overlapping buffers, since they minimise the scale effect compared to contiguous grids. One may recommend a two-step process: (a) estimate the change in the EDR using the scale area approach (e.g. as in Table 1) and (b) if some discrepancy is observed as a function of scale, choose which interval limit is best suited given the conservation context of the population (see below).

To assess the status of small recovering populations like wolves in France, conservative estimates of the colonisation process are preferable, especially when presence-only data

are used, and when false negative or positive detections may occur (Rondini et al. 2006). Balancing the risk of over estimating EDR (i.e. including false positives) versus under estimating it (i.e. discarding false negatives) is a big issue. However, wolf is a cryptic species that lives at low density, so presence signs are not easily detected. Of course the different sign categories are not equally reliable: for example, non-invasive genetics are more robust to mis-identification than sightings. Assessing EDR based only on hard facts such as genetic proofs is tempting, but would result in too conservative an estimate, a socially unsustainable strategy. A more balanced approach would consider all categories of validated presence signs provided the validation process is conservative. In the present work, ca. 40% of the detected presence signs (prints, preys and sightings) were discarded. Such a high rejection rate is likely to produce conservative estimates of the species' range. In addition, the detection probability of the different categories is probably not uniform over the distribution range of the wolf: scats are easily found—and genetically validated—in wolf permanently occupied areas, whereas sightings are often reported—and discarded—first at the colonisation front of the species. Such a spatial heterogeneity in detection and validation rates as a function of sign categories may result in an underestimated range too. Finally, because of a limited sampling effort beyond the limits of the already documented wolf range, the estimated changes are probably conservative. The sensitivity of the estimated range changes to category-specific differences in detection and validation rates is likely weak since one can reasonably assume theses differences to be constant over time. This assumption has nevertheless to be further investigated. To consider the possible resulting biases, particularly when the colonising process is slow during the focus period, larger CAUs should be preferred for monitoring yearly changes in the EDR as they will probably allow a better perception of a low recovery rate.

In well-established wolf populations, growth rates are usually weak (see Salvatori and Linnell 2005 for a European-wide review), but conflicts with human interests may be sharp due to large numbers of wolves. If active management (sensu Linnell et al. 2007) is implemented, including lethal control, targeting a maximum and still sustainable legal yield of wolves (Chapron et al. 2003; Chapron 2004) may be perceived by stakeholders as a balanced strategy. Using over-smoothed population indicators in such contexts (such as EDR changes estimated with large CAU) may however result in unbalanced management options: the speed of the colonising process would then be underestimated, which could lead to conservative decisions (e.g. an underestimated possible yield of wolves). Stakeholders usually look for a balanced treatment of competing claims (e.g. hunters, farmers, nature conservationists, see

Giller et al. 2008) and active management aims at improving the social acceptance of the species. So estimating short-term changes in the EDR from small-sized CAUs may be the right option to select under these circumstances.

However, the scale effect on the trends in EDR was weak in our study (less than 15% variation between cell areas of 6 and 100 km^2), especially with circular buffers. Overall, our results are likely to be dependent on the interaction between the characteristics of dispersal within the studied population and the size of the cell area. The relative occurrence of long- and short-distance dispersal will affect the sensitivity of the mapping process to changes in the range of the species. The colonising process within the French wolf population is partly based on long-distance dispersal (Valière et al. 2003), and this obviously interacts with the mapping process. Theoretically speaking, one should therefore use a large and circular cell area rather than a grid for monitoring changes in the range of such a wolf population. This buffering system is less sensitive to scale effects, whether short-term or long-term variations in the species' range are concerned.

Conclusion

Practically speaking, much has already been done in the world of conservation biology using grid-based representations that are more or less standardised. The IUCN guidelines (IUCN 2008) emphasise that "…the choice of scale at which [EDR] is estimated may influence the outcome of Red List assessments and could be a source of inconsistency and bias", for example if scale is inappropriate to the species' characteristics. They further suggest that estimating the EDR "…may require standardisation to an appropriate reference scale to reduce such bias", and propose a toolkit for computing ad hoc scale correction factors.

Considering the French recolonising wolf population (Cubaynes et al. 2009), we are mostly concerned with scale-related bias when assessing the changes in the EDR over years. Indeed, the instructions for reporting species' status under article 17 of the Habitats Directive put some emphasis on estimating changes in the EDR. Estimating the value of a species' range at a given point in time is one thing, evaluating the changes in the range over time is another. Since the actual range value is always unknown, one is bound to compare estimates over time to assess possible trends. The challenge, given that the E.C. Habitats Committee suggests using the E.E.A. 10×10-km cell grid, is to balance the need for merging diagnoses between areas (or countries) against the need for robustness of the intra-area diagnosis. On one hand, grid-based maps using a fixed

scale cell area are widely used for monitoring changes in species' range; on the other hand, our results suggest that other mapping approaches may be less prone to over- or under-estimation of changes in the range. We suggest a two-step approach to solving this apparent paradox. First, the classical grid-based method could be used as a coarse-grained approach to changes in the range of large transboundary populations (sensu Linnell et al. 2007), for assessing global trends. Second, a scale-dependent method using circular buffers could be implemented as a fine-grained approach to changes in the range of local population segments (e.g. animals contained in one of the countries that share a transboundary population), for assessing the local trend.

The focus of mandated monitoring (sensu Lindenmayer and Likens 2010) is usually to identify coarse patterns such as large-scale trends in population numbers and distribution. However, having some knowledge about the biological process that underlies the observed trend is crucial to select the most appropriate approach. Since wolves are known to combine both short- and long-distance dispersal while recolonising (e.g. Kojola et al. 2006), even a descriptive approach like basic mapping of the detected presence may face some hidden pitfalls like scale/shape effects in interaction with the species' characteristics.

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