REVIEW

The sizes of species' geographic ranges

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Summary

1. Geographic range size and how it changes through time is one of the fundamental ecological and evolutionary characteristics of a species, and a strong predictor of extinction risk. However, the measurement of range size remains a substantial challenge. Indeed, there is significant confusion in the literature as to how this should be done, particularly in the context of the distinction between the fundamentally different concepts of extent of occurrence (EOO) and area of occupancy (AOO), and the use of these quantities, including in assessments of the threat status of species.

2. Here we review the different approaches to determining the geographic distributions of species, the measurement of their range sizes, the relationships between the two, and other difficulties posed by range size measurement (especially those of range discontinuities when measuring EOO, and spatial scale when measuring AOO).

3. We argue that it is important to (i) distinguish the estimation of the distribution of a species from the measurement of its geographic range size; (ii) treat measures of EOO and AOO as serving different purposes, rather than regarding them as more or less accurate ways of measuring range size; and (iii) measure EOO including discontinuities in habitat or occupancy.

4. *Synthesis and applications*. With the availability and collation of extensive data sets on species occurrences, a rapidly increasing number of studies are investigating geographic range size, and particularly how various measures of range size predict macroecological patterns and inform assessments of the conservation status of species and areas. The distinction between EOO and AOO is becoming blurred in many contexts, but most particularly in that of threatened species assessments for Red Listing. Continued progress in these fields demands greater clarity in the meaning and derivation of measures of geographic range size. The two principal measures serve different purposes, and should not be regarded as alternatives that simply differ in accuracy.

Key-words: area of occupancy, extent of occurrence, geographic distribution, range limits, Red List

Introduction

Geographic range size, and how it changes through time, is one of the fundamental ecological and evolutionary characteristics of a species (Gaston 2003). Perhaps most immediately, however, range size is a strong predictor of extinction risk. Reflecting the vulnerability of narrowly distributed species, range size plays a key role in categorizing species according to their short-term likelihood of extinction, including listing on the IUCN Red List of threatened species, and thus contributes importantly to indices of global trends in threat status and to the prioritization of species for conservation effort (IUCN 2001; Baillie, Hilton-Taylor & Stuart 2004). Indeed, of the 4440 threatened species in groups for which

Red List assessment is complete, or nearly so, some 2072 (47%) are listed on the basis of geographic range criteria alone, and about 75% of threatened amphibians are listed solely on range measures (IUCN criteria B1 or B2; Table 1). These figures are conservative because range size may also be used to list species under criterion A, as an indicator of a high rate of past or projected population decline, or criterion D, as an indicator of a very small or restricted population (Standards and Petitions Working Group 2006).

This said, the measurement of geographic range size is not straightforward (Rapoport 1982; Gaston 1991, 1994a, 2003). Gaston (1991) distinguished two different kinds of measure. Extent of occurrence (EOO) is that area which lies within the outermost geographic limits to the occurrence of a species, and the area of occupancy (AOO) is that within those outermost limits over which it actually occurs. This distinction is

Table 1. The use of geographic range size criteria (B1 or B2) in IUCN Red Listing in the four higher taxa with complete or near-complete evaluation in 2007. Species listed under criterion B qualify on the basis of a small 'Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both' (IUCN 2001). Note that where species satisfy the range size thresholds, they must also meet at least two of three subcriteria relating to (i) severe fragmentation, (ii) continuing decline in range size, population size or habitat extent, or (iii) extreme fluctuations in range size, population size or habitat extent

Taxon	No. of spp. described*	No. of spp. evaluated by 2007	No. of spp. threatened in 2007	No. of threatened spp. qualifying under at least one geographic range criterion	No. of threatened spp. qualifying only under geographic range criteria
Mammals	5416	4863 (90%)	1094 (22%)	481 (44%)	380 (35%)
Birds	9956	9956 (100%)	1217 (12%)	481 (40%)	254 (21%)
Amphibians	6199	5915 (95%)	1808 (31%)	1425 (79%)	1351 (75%)
Gymnosperms	980	909 (93%)	321 (35%)	143 (45%)	87 (27%)
Total	22 551	21 643 (96%)	4440 (21%)	2530 (57%)	2072 (47%)

*all data from IUCN (2007).

Table 2. EOO vs. AOO in IUCN threat listing. Thresholds for EOO are 100 km², 5000 km² and 20 000 km² for Critically Endangered, Endangered and Vulnerable, respectively, while the equivalent figures for AOO are 10 km², 500 km² and 2000 km²

Taxon	No. of threatened spp. qualifying under at least one geographic range criterion	No. of these that use EOO only	No. of these that use AOO only	No. of these that use both measures of geographic range size
Mammals	n/a*			
Birds	481 (40%)	216 (45%)	26 (5%)	239 (51%)
Amphibians	1425 (79%)	895 (63%)	157 (11%)	373 (26%)
Gymnosperms	143 (45%)	5 (3%)	7 (5%)	131 (92%)

*The 2007 mammal assessment uses 1994 IUCN criteria, which do not distinguish EOO and AOO.
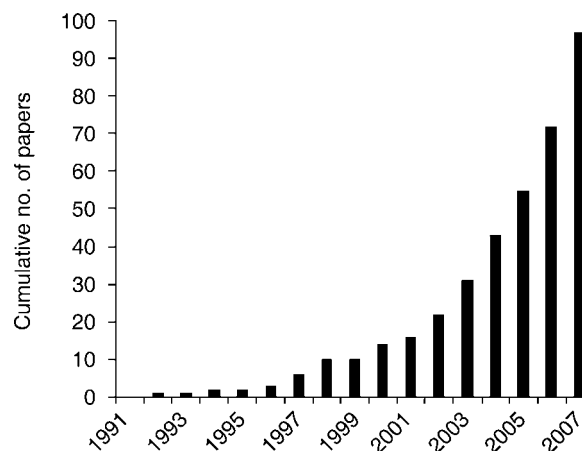
Fig. 1. Cumulative number of papers explicitly employing EOO or AOO measures since the metrics were first defined in 1991. Data retrieved from the Web of Science (http://isiknowledge.com/) on 28 March 2008, using the search term 'extent of occurrence' OR 'area of occupancy' in the article title or abstract. Articles retrieved were filtered manually to ensure that all in the final list related to species geographic range size measures.

now employed widely in both pure and applied contexts (Fig. 1). From a conservation perspective, the two measures are formally distinguished in relation to IUCN Red Listing (IUCN 2001; Standards and Petitions Working Group 2006). Many threatened species are categorized based only on EOO,

although categorizations for about half of the birds and over 90% of the gymnosperms use both EOO and AOO (Table 2). As the usage of these geographic range size measures has increased, the importance of long-standing problems in quantifying EOO and AOO has become more apparent, and fresh issues have emerged. Here, we review these challenges, their consequences, and progress made toward resolving them.

Determining species' distributions

Measures of geographic range sizes depend on information about the spatial distributions of species. However, it is important to distinguish the process of determining those distributions from that of measuring range sizes. The two are frequently confounded, despite the fact that some kinds of distributional data will be more appropriate for estimating EOO or AOO. Indeed, it is at the intersection between the methods used to determine the distributions of species and those used to estimate their range sizes that many of the most important issues with the latter arise.

The distributions of species have variously been determined by these five broad groups of methods:

Marginal occurrences. Distributions have long been estimated through mapping locality records that are at, or presumed to be at, the outermost geographic boundaries to a species' occurrences (their range limits), and interpolating between to delineate these boundaries (Hall & Kelson 1959). A broad representation of the occurrence of a species results, typically

in the form of an irregular, largely contiguous surface. Early maps of this kind were undoubtedly extremely approximate, with low ratios of genuine observational data to interpolation. However, the maps in many modern field guides and monographs are often based on painstaking collations of existing marginal locality records, and the informal interpolation of geographic ranges is based to varying degrees on knowledge of environmental conditions and expert opinion. Debate may often accompany any significant errors (Winker 1995; Beason 2002). The physical size at which such maps are typically printed in publications should not be confused with that of the originals from which they may derive. Because they intentionally ignore the detailed internal structure of species' distributions, excepting perhaps major discontinuities, maps generated from marginal occurrences tend to exhibit much greater errors of commission (false occurrences) than of omission (false absences; Gaston 1991; Graham & Hijmans 2006).

Habitat distributions. Maps of preferred habitats or combinations of environmental conditions have commonly been used to estimate the geographic distributions of species. At its simplest, this has involved mapping the distribution of the habitat type(s) used by a species, or of areas falling within the appropriate ranges or classes of one or more environmental variables within which it has been recorded as occurring. Sometimes, the state of different environmental variables is converted into a suitability score, and such scores combined across variables to generate synthetic habitat suitability surfaces (Rondinini, Stuart & Boitani 2005; Kaschner *et al.* 2006; Rondinini & Boitani 2007; Boitani *et al.* 2008). Alternatively, the occurrence of suitable habitat may be known for some locations, and its wider distribution may then be statistically modelled based on environmental variables (Early, Anderson & Thomas 2008). Such exercises implicitly contain some original information about the local occurrences of the species in that this underpins the information on environmental preferences. However, they may use no spatially explicit occurrence data in generating the suitability surfaces. This said, recognizing particularly that other processes may be important in limiting species' geographic distributions, habitat suitability surfaces are often intersected with, or examined within, the bounds to marginal occurrences (Rondinini *et al.* 2005; Rondinini & Boitani 2007; Harris & Pimm 2008). The distributions predicted by habitat suitability surfaces may be tested using local occurrence data (Rondinini *et al.* 2005; Rondinini & Boitani 2007). In general, habitat distribution approaches tend to result in greater errors of commission than omission in the actual overall occurrence of species, because many factors may further limit distributions.

Range-wide occurrences. Where a sufficient density of locality records is available for the region of interest, a species' distribution can be estimated on this basis alone. Given that this density is seldom high, records are often generalized to rather larger areas by mapping them into the cells of an equal area grid. This is the basis on which many distribution atlases have been constructed (Gibbons *et al.* 2007). In the main, distributions based on range-wide occurrences suffer from

greater errors of omission than commission, with sampling effort seldom adequate except at coarse mapping resolutions and often inadequate at any resolution that is useful for many applied purposes (Graham & Hijmans 2006; Rondinini *et al.* 2006). Grid-based occurrences may sometimes be informally interpolated (i.e. without using a statistical model) on the basis of habitat types to reduce this problem, or formally interpolated using patterns of sampling effort (Högmander & Møller 1995).

Statistical modelling. Statistical modelling approaches can help reduce the level of omission errors in distributions determined directly from range-wide occurrence data. These inductive models predict species' distributions using a combination of presence/absence or presence-only locality records (in their raw form or generalized on a grid), data on spatial variation in environmental variables, and one or more modelling techniques (e.g. logistic regression, GLM, GARP, MaxEnt: Guisan & Zimmerman 2000; Stockwell 2007; Phillips & Dudík 2008). Many such models have employed small numbers of original locality records (Hernandez *et al.* 2006; Pearson *et al.* 2007), and some have attempted to use coarse-grained occurrence data to predict distributions at finer resolutions (Collingham *et al.* 2000; Araújo *et al.* 2005; McPherson, Jetz & Rogers 2006). Statistical models tend to overestimate the distributions of species, as they focus on macro-environmental rather than micro-environmental factors (both may be important in determining where species occur), pay no explicit attention to species interactions (although this may be implicitly accounted for) nor to historical constraints and contingencies (Gaston 2003). That is, commission errors tend to exceed omission errors, although the latter may be inflated if the distribution of known occurrence records is highly biased and the range of environmental conditions occupied not well sampled (Graham & Hijmans 2006; Loiselle *et al.* 2008). Again, commission errors may be reduced by intersecting predicted occurrences with, or only examining them within, the bounds to a species' marginal occurrences (Loiselle *et al.* 2003).

Process-based modelling. 'First principles' models, rooted in ecophysiological traits of species and environmental conditions have been used to generate predictions of distributions (Porter *et al.* 2002; Kearney & Porter 2004; Morin, Augspurger & Chuine 2007). To varying degrees, these use physical principles to determine how the interaction of the characteristics of an organism with microclimatic conditions shape mass and energy balances, and thence the occurrence of the species. Whilst typically run for the broad region in which the species is known to occur, or thought likely to spread, such models may otherwise assume no information about its spatial occurrence. Commission errors tend to exceed omission errors, although the former may be reduced by including progressively greater detail on the abiotic and biotic environment.

Although often characterized simply as differing in the accuracy of their predictions, the outcomes of these various methods of determining species' distributions are better thought of as differing in the characteristics of those distributions that they are attempting to represent. Methods based

Table 3. Conditions under which geographic distributions estimated using different methodological approaches provide an accurate basis for subsequently measuring EOO or AOO

	EOO	AOO
Marginal occurrences	If good sampling of margins	Only if species distributed across much of area within range margins, and thus typically narrowly distributed
Habitat distributions	If habitat use well understood and mapped, but may often provide a poor basis, especially if habitat use changes toward margins	If habitat use well understood and mapped, but typically indicates potential rather than actual area of occupancy
Range-wide occurrences	If sampling extensive	If sampling intensive
Statistical modelling	If species' distribution well estimated by environmental variables, but typically indicates potential rather than actual extent of occurrence; estimate will be improved by careful choice of cut-off point for predicted probabilities of occurrence	If species' distribution well estimated by environmental variables, but typically indicates potential rather than actual area of occupancy; estimate will be improved by careful choice of cut-off point for predicted probabilities of occurrence
Process-based modelling	If species' distribution well estimated by biophysical variables, but typically indicates potential rather than actual extent of occurrence; estimate will be improved by careful choice of cut-off point for predicted probabilities of occurrence	If species' distribution well estimated by biophysical variables, but typically indicates potential rather than actual area of occupancy; estimate will be improved by careful choice of cut-off point for predicted probabilities of occurrence

on marginal occurrences capture the outermost limits and sometimes estimate these better than any other approach, particularly when lots of peripheral locality data are available. Methods based on range-wide occurrences tend to capture overall distributions better than other approaches when geographic ranges are small and locality information plentiful, or when locality information is well dispersed and widely generalized. When derived from systematic surveys they may often be quite good in identifying marginal occurrences. Methods based on habitat suitabilities and statistical modelling attempt to predict the potential distribution of a species within the limits of its occurrence. They tend to work well when historical factors, dispersal limitation and sampling biases are not dominant processes, although some of these effects can be reduced by careful evaluation of alternative models, and consideration of how the results will be applied (Loiselle *et al*. 2003). Process-based modelling exercises provide surprisingly good predictions of distributions when constrained to regions in which the species are a priori known to occur and when sufficient detail is known about ecophysiological traits.

Having at some level established the distribution of a species, one can proceed to measure its range size, in terms either of its EOO or its AOO.

Extent of occurrence

EOO captures the overall geographic spread of the localities at which a species occurs. It is emphatically not a measure of the area over which it is actually found to occur (although it may approach this for some species). EOO is thus included amongst IUCN Red List criteria as a general metric of the degree of risk spreading amongst the occurrences; the larger the EOO, the less likely that all localities will undergo simultaneous extinction as a consequence of stochastic, or indeed many directional, pressures (Standards and Petitions Working Group 2006).

EOO measures have most commonly been calculated as the area that lies within some generalized estimation of the position of the outermost boundary to a species' distribution, where this boundary is an irregular contiguous line, typically determined from the interpolation of marginal occurrences. However, more formal methods have also been applied, including calculation of the area that lies within (i) a minimum convex polygon or convex hull embracing the occurrences of a species (Shaw, Musina & Gichuki 2003; Standards and Petitions Working Group 2006; Miller, Enright & Lamont 2007; Sérgio *et al*. 2007; Sheth *et al*. 2008); (ii) an α–hull constructed by building a Delauney triangulation of the occurrence points, and removing connecting lines longer than a certain multiple of the average line length, thus deleting areas spanning largely unoccupied regions (Burgman & Fox 2003; Farnsworth & Ogurcak 2006; Sérgio *et al*. 2007); or (iii) an interpolated threshold of relative or absolute abundance (MacArthur 1972; Root 1988). These different methods can give markedly different estimates of EOO.

EOO measures can in principle be derived from the distributions of species estimated using any of the five groups of methods, although the latter can of course differ substantially in how well they estimate the outermost limits to the distribution of a species (Table 3). Those based on marginal occurrences will generally be most accurate, providing there is sufficient sampling effort. Those based on range-wide occurrences will estimate outermost limits to varying degrees of accuracy, depending on sampling density and the size of the areas over which known occurrences are generalized (e.g. grid cell size). Where sampling density is low, these areas may need to be very large, resulting in uncertain range limits. Habitat distributions, statistical modelling and process-based modelling can result in highly variable estimates of the position of the distributional limits of any given species, depending on the relationships between the factors actually determining those limits, the factors that are included in making the estimation, and the spatial resolution.

For a given representation of the distribution of a species (derived from any one of the five groups of methods), the key issue in measuring EOO, and hence in evaluating the strengths and weaknesses of different approaches, is how to treat discontinuities in occurrences. As formally defined above, no matter how large, discontinuities are included within the EOO. From the earliest discussions of the measure, it was recognized that this may result in the inclusion of substantial areas of entirely unsuitable environment (e.g. areas of ocean for a terrestrial species or areas of land for a marine one; Gaston 1991, 1994a). Various qualifications have been suggested to limit the extent to which this occurs. The IUCN (2001) Red List criteria state that measures may exclude 'discontinuities or disjunctions within the overall distributions of taxa'. However, the associated guidelines indicate that the 'exclusion of areas forming discontinuities or disjunctions from estimates of EOO is discouraged except in extreme circumstances, because disjunctions and outlying occurrences accurately reflect the extent to which a large range size reduces the chance that the entire population of the taxon will be affected by a single threatening process' (Standards and Petitions Working Group 2006).

Debate about the relative merits of different methods of measuring EOO has typically focussed on the degree to which major discontinuities are included or excluded. For example, Burgman & Fox (2003) favour the use of α–hulls over convex polygons, because the former provide an explicit means for excluding discontinuities. They use simple hypothetical distribution shapes to explore the implications of different methodologies. Of these, a horseshoe- or u-shape is perhaps most revealing. A minimum convex polygon essentially measures the area within the square or rectangle formed by the outermost corners of this distribution, whilst an α–hull tends more closely to trace the bounds of the horseshoe.

Some have criticized EOO measures for failing to account for habitat discontinuities at much finer scales, particularly those resulting from fragmentation (e.g. Harris & Pimm 2008; Jetz, Sekercioglu & Watson 2008). We argue that reducing measured EOO by removing areas in which the species does not actually occur, pushes such measures away from EOO and toward AOO. Indeed, it appears that some authors are labelling AOO as EOO in conservation assessments. For example, Lewison & Oliver (2006) observe with regard to the pygmy hippopotamus *Hexaprotodon liberiensis*, 'The current evidence suggests that the geographic range (as measured by extent of occurrence) is severely fragmented and is continuing to decline in area, extent and quality'. Describing the geographic range of *Acacia anegadensis*, endemic to Anegada Island in the Caribbean, Clubbe *et al*. (2003) state that the 'area of the island is 38 km^2, of which approximately one third is water in the form of salt ponds. Therefore extent of occurrence for *Acacia anegadensis* is approximately 25 km^2'. Sillero-Zubiri & Marino (2004) calculated the EOO for the Ethiopian wolf *Canis simensis* as '4200 km^2 [defined as area above 3000 m asl]' (a.s.l., above sea level), and with regard to the wreckfish *Polyprion americanus*, Sadovy (2003) notes that 'The extent of

occurrence could probably be estimated by calculating the area of potential habitat'.

Given the diversity of forms that geographic distributions can take, and thus the difficulties of establishing some threshold at which discontinuities should be excluded that is likely to be generally appropriate, it seems both simplest and most logical to stipulate that EOO should always be measured including these discontinuities. This retains a clear distinction of purpose between EOO and AOO measures. Attempts to remove discontinuities need to state explicitly how these improve estimation of the overall distributional extent of a species, rather than simply more closely approximating its AOO.

Area of occupancy

By definition, the AOO of a species is equal to or less than its EOO (although depending on the combination of measurement approaches used this may not in practice always be so). Typically, it is much smaller, and sometimes only a tiny fraction of the EOO (Roberts & Hawkins 1999; Goehring *et al*. 2007; Hurlbert & Jetz 2007; Boitani *et al*. 2008). AOO has been used as a criterion for IUCN Red Listing because it provides a general measure of how robust the distribution will be to stochastic and directional threatening processes, and of the relative population sizes of species (with both the area occupied by a species and its population size contributing to its risk of extinction; Gaston 2003). AOO will tend to be markedly better correlated with population size than is EOO.

As with EOO, AOO has been calculated in a variety of different ways, which can give markedly different estimates. The commonest approach is to calculate the area of distributions determined from range-wide occurrences, usually generalized on a grid (Randrianasolo, Miller & Consiglio 2002; Riba *et al*. 2002; Litvaitis *et al*. 2006; Harris *et al*. 2007; Sheth *et al*. 2008). Other methods have included using the fraction of sampled sites within the EOO at which the species occurs (Goehring *et al*. 2007; Van der Veken *et al*. 2007; Jetz *et al*. 2008), the summed area used by local populations (Cowley *et al*. 1999), habitat suitability (Good, Zjhra & Kremen 2006; Reisinger, Stuart-Fox & Erasmus 2006; Jetz, Wilcove & Dobson 2007; Boitani *et al*. 2008), and various methods of spatially clustering and buffering locality records (Rapoport 1982; Hernández & Navarro 2007).

As with EOO, AOO measures can in principle be derived from the distributions of species estimated using any of the five groups of methods, and just as with outermost limits they can also differ substantially in how well they estimate its occurrence within those limits (Table 3). Those based on marginal occurrences will typically be least accurate, except where all occurrences are highly aggregated, as with some very restricted species. Those based on range-wide occurrences will estimate occupancy to varying degrees of accuracy, depending on sampling density and the size of the areas over which known occurrences are generalized (e.g. grid cell size). Habitat distributions, statistical modelling and process-based modelling can result in highly variable occupancy estimates,

depending on the relationships between the factors actually determining those limits, the factors that are included in making the estimation, and the spatial resolution.

The single biggest challenge in measuring AOO is that the outcome is heavily dependent on the spatial resolution both of the distribution data and the method of measurement employed (Gaston 1991, 2003; Keith *et al*. 2000; Willis, Moat & Paton 2003). Where underlying distribution estimates are poorly spatially resolved, represented in the extreme by maps of marginal occurrences, it is difficult to discriminate occupied and unoccupied areas within the EOO (although at finer resolutions, the position of the outermost boundary to the distribution becomes increasingly well resolved). It is then impossible, or virtually so, to measure anything other than effectively the EOO of a species from its distribution data. This is also true when the distributions of species have been estimated from low-resolution habitat maps, from occurrences generalized to low-resolution grid cells, or have been statistically modelled at low spatial resolutions (again emphasizing the significance of the intersection between the methods used to determine the distributions of species and the measures used to estimate their range sizes).

Where the underlying distribution estimates are spatially better resolved, such that discontinuities and disjunctions are apparent, the finer the resolution at which these are mapped, the more area that will be found to be unoccupied (Gaston 1991, 1994b; Cowley *et al*. 1999; Goehring *et al*. 2007). There is then an important interplay between the resolution at which distributions are mapped and that at which AOO is estimated (Shaw *et al*. 2003). In the limit, the AOO of an immobile species is defined by the summed area of the instantaneous localities of all (or just mature) individuals, whilst the AOO of a mobile species may alternatively be the summed area of the home ranges of these individuals (Gaston 1991). Given that the occurrence of all individuals is known only for a handful of species, distributions tend to be determined at a spatial resolution that either enables existing locality records to be appropriately generalized or their appropriate interpolation (informal or formal).

AOO has been measured by generalizing data or models at a wide variety of spatial resolutions, from 1 km^2 (Bernardos, Amado & Amich 2006; Solano & Feria 2007) to more than 10 000 km^2 (Fig. 2; Habib, Wiersma & Nudds 2003; Riba *et al*. 2002); note that at coarser resolutions, the estimated AOO may be larger than the estimated EOO, violating the definitional necessity that the converse is true. The relationship between the AOO of a species and the spatial resolution at which this is measured has been termed a scale-area (Kunin 1998; Standards and Petitions Working Group 2006) or range-area relationship (Ostling *et al*. 2003). The form that such relationships take remains somewhat contentious. Authors have variously argued that the scaling is fractal, fractal over particular ranges of spatial resolutions, close to fractal, fractal-like, not fractal at all, or follows a more generic scaling termed a generalized fractal (Gaston 1994b; Kunin 1998; Lennon, Kunin & Hartley 2002; Hartley *et al*. 2004; Pocock *et al*. 2006; Storch *et al*. 2008).
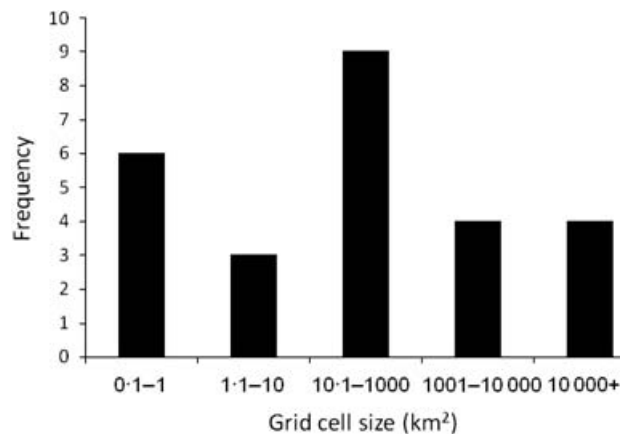
Fig. 2. Frequency distribution of grid cell sizes at which studies have measured AOO. Forty-seven studies were investigated, of which seven used polygon or non-spatial methods to estimate area of occupancy, and 14 provided no clear statement of grid cell size. The remaining 26 studies are shown in the figure.

In practice, limitations of data availability notwithstanding, the grain size used should be biologically appropriate for a particular taxon (IUCN 2001). For example, a locally dispersing plant might occupy only a small fraction of a 1×1 km square, and dispersal capabilities across taxa range from a few centimetres to hundreds of kilometres (Keith 1998). Study grain size is intimately tied up with the absolute magnitude of the resulting AOO estimate, and whether IUCN Red List thresholds are met will depend to a large extent on the interaction between sampling intensity and the scale used to measure AOO (Keith *et al*. 2000). Guidelines for applying IUCN criteria suggest that 2×2 km may often be appropriate, and is recommended as a suitable reference scale (Standards and Petitions Working Group 2006); note that a resolution greater than $3 \cdot 2 \times 3 \cdot 2$ km prevents categorization as critically endangered on the basis of AOO, because the resulting estimate will always be ≥ 10 km^2. Being more prescriptive is obviously difficult, given variation in the quantity and quality of underlying distribution data, and in the biologies of species. Ideally, thresholds would vary systematically depending on these biologies and the extinction risks associated with different AOO; however, no method of determining such variable thresholds presently exists.

The temporal span over which locality records are assembled will also influence measures of AOO, with many species having lost or gained occurrences within their distribution regardless of whether the range limits have shifted. Declining species often show sparse, fragmented distributions whilst increasing species occupy their geographic range more densely, reflecting the dominant processes of extinction and colonization, respectively (Wilson *et al*. 2004).

Choosing range size measures

EOO and AOO represent fundamentally different aspects of geographic range size. Nonetheless, some authors have

regarded measures of EOO as poorer or less accurate than those of AOO (e.g. Hurlbert & Jetz 2007; Miller *et al.* 2007; Jetz *et al.* 2008). For example, EOO has variously been described to 'overestimate the species' current range' (Shaw *et al.* 2003), to 'overestimate the area of occupancy' (Jetz *et al.* 2007), and to be 'unnaturally stretched' (Shaw *et al.* 2003). We believe that a clear distinction between the two measures is important for at least three reasons. First, it separates the determination of species' distributions from that of measuring their range sizes. The choice of range size measure should be made independently of efforts to map distributions, because either class of range size measure can be calculated from most methods used to map species' distributions (Table 3). Second, useful differences between alternative metrics of geographic range size can be obscured by simply viewing AOO as a more accurate version of EOO. The two range size measures serve different purposes, and the use to which they will be put is crucial in deciding which to employ. Third, assessments of conservation priority can be confused if the metrics of EOO and AOO are treated as essentially attempts to achieve the same endpoint (e.g. estimate the magnitude of a particular threatening process). From both theoretical and applied perspectives, the two classes of measures have entirely different interpretations that emphasize different aspects of geographic range size and hence, extinction risk.

EOO explicitly measures the overall geographic spread of the localities at which a species is found, and not the area over which it actually occurs. Particularly where species are limited to individual land masses or ocean basins, EOO is typically used to understand the factors determining species' distributional limits, or in studying geographic range dynamics. EOO is also used as a general measure of the likelihood that all localities at which a species occurs will undergo simultaneous extinction. It is used overwhelmingly in IUCN Red List assessments that involve measures of geographic range size (Table 2). Perhaps in part, this reflects concerns about data quality, because measures of occupancy are not feasible at a sufficiently fine spatial grain to reduce overestimation errors to acceptable levels. The IUCN (2001) criteria for Red List assessments recognize this in allowing both EOO and AOO measures to be used. Although there is discussion about the implied spatial scale of these thresholds (Keith *et al.* 2000), and the fixed 10 : 1 ratio between EOO and AOO thresholds (Jetz *et al.* 2008), at least these enable the degree of spatial risk spreading and magnitude of the occupied area to be assessed independently, which will be crucial in assessing extinction risk in some cases.

For some purposes, it is neither EOO nor AOO *per se* that is of interest, but rather the difference between the two for a particular species, or the relationship between the two for an assemblage. This relationship is constrained broadly to be triangular, because AOO can only exceed EOO under very particular circumstances. However, recent range size estimates of threatened birds show a great deal of scatter, with AOO estimates falling anywhere within the range of possible values derived from EOO (Fig. 3). Here, small AOO relative to EOO typically concerns colonial species such as pelagic seabirds
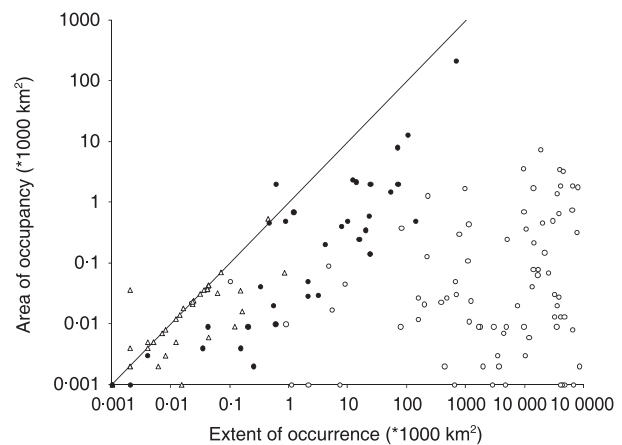
Fig. 3. Relationship between breeding EOO and AOO estimates for the 152 species of threatened birds where both have been estimated. Open circles represent colonial seabirds, open triangles other species restricted to a single island or mountaintop, and filled circles the remaining species. Solid line indicates a 1 : 1 ratio between the two measures. From left to right, the two species where estimated AOO greatly exceeds estimated EOO are Calayan rail *Gallirallus calayanensis* and Bahia antwren *Herpsilochmus pileatus*, both narrowly distributed resident species. Data from BirdLife 2008 list of threatened birds (http://www.birdlife.org, accessed 27 May 2008).

where birds take long foraging trips from breeding colonies. Ratios closer to unity are concentrated toward narrowly distributed species (Fig. 3) such as those endemic to a single island or mountain. The proportion of the EOO that is occupied has been explored in a number of contexts (Dennis & Shreeve 1991; Goehring *et al.* 2007; Hurlbert & White 2007). To discriminate it from the different measures of range size, it can usefully be termed range fill.

Whilst the choice of EOO over AOO will occasionally be forced by data quality, we doubt that removing apparently unoccupied discontinuities ever constitutes a useful adjustment to an EOO estimate. Because such attempts are aimed at revealing within-range occupancy patterns, removals of unoccupied areas from an EOO are in our view best treated as measures of AOO. AOO will generally be correlated with population size, and provide a useful estimate of extinction probability based on changes in within-range habitat extent, fragmentation or suitability, and demographic processes (Joseph & Possingham 2008). Certainly, studies comparing EOO with AOO have found differences in the identification of species of conservation concern (Goehring *et al.* 2007; Harris & Pimm 2008; Jetz *et al.* 2008). These results reinforce the importance of explicitly stating the type and purpose of a geographic range size estimate.

Concluding remarks

With the availability and collation of extensive data sets on species' occurrences, a rapidly increasing number of studies are investigating geographic range size, and particularly how various measures of range size predict macroecological patterns and inform assessments of the conservation status of

species and areas. We believe that there is significant confusion in the literature over the measurement and interpretation of geographic ranges, and are concerned that the distinction between EOO and AOO is becoming blurred in many threatened species assessments for Red Listing. The two measures serve different purposes, and should not be regarded as more or less accurate ways of measuring range size. We take the view that EOO should always be measured including any discontinuities in habitat or occupancy. This is particularly important in threatened species assessments, where its primary purpose is to measure the degree of spatial risk spreading. The choice of range size measure should be made independently of efforts to map species' distributions, and we reiterate that there should be a clear distinction between modelling species' distributions and measuring their range sizes.

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