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Predicting home range use by golden eagles *Aquila chrysaetos* in western Scotland

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The conservation and management of golden eagles *Aquila chrysaetos* requires information on home range, which is expensive and time-consuming to collect. We describe modelling techniques for predicting golden eagle ranging behaviour within a Geographic Information System (GIS). The model, called PAT (Predicting Aquila Territory), used data on ranging behaviour and geospatial factors from two areas of western Scotland. A range centre was estimated from the weighted mean nest site location in the past ten years. Range boundaries were estimated from Thiessen polygons, in the presence of neighbouring ranges, and a maximum ranging distance generated from parameters responsive to local range density, in the absence of neighbouring ranges. The model assumed that eagles did not use the sea or freshwater bodies, and avoided areas of human activity and closed canopy forests. The model also assumed that golden eagles preferred areas close to ridges (and other convex terrain features) and close to the centre of the range. The model output, at 50 × 50 m resolution, was three-dimensional with geographical location as *x* and *y* co-ordinates and use as a percentage of total home range use as the *z* co-ordinate. Comparison of the model's predictions against range use observations suggested that it provided a good fit to observed range use. The PAT model has many potential applications, including the prediction of the likely impact of local developments such as windfarms and commercial forest expansion on territorial eagles and for providing information useful to managing land use change to the benefit of eagles across large areas.
Keywords: golden eagle, *Aquila chrysaetos*, GIS, home range, modelling.

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Breeding pairs of golden eagles *Aquila chrysaetos* occupy large home ranges, portions of which are actively defended seasonally as an exclusive territory (Watson 1997). Like many large raptors the golden eagle is vulnerable to human influences, such as land-use changes, and rural developments can have a negative impact (Newton 1979, McGrady 1997, Watson 1997, Pedrini & Sergio 2001a, 2002).

Features of the ecology of the golden eagle make it difficult to achieve eagle conservation aims, particularly within human-influenced landscapes. Land managers must sometimes make decisions about the likely effects of land use change on eagles. These decisions must be made within a limited time period or be applied across a large area, precluding the collection of field observations that describe actual range use. In addition, it is time-consuming and expensive to research golden eagle ranging behaviour because the birds mainly occur at low densities in remote mountainous country (Watson 1997). Moreover, agencies responsible for the protection of eagles are often reactive, so the rapid identification of important areas for golden eagles would allow them to be incorporated much earlier into the process of planning developments (McGrady et al. 1997). This would reduce conflict between developers and conservation agencies, lower planning costs, and minimise the possibility of inappropriately placed developments (Brendel et al. 2002, McLeod et al. 2002).

Because it is difficult and expensive to obtain detailed range use data it would be helpful if a model could be developed that used readily available habitat data to predict range usage and, therefore, identify those areas that are important for golden eagles. Here we describe the development of a rule-based model for predicting golden eagle ranging behaviour using a Geographic Information System (GIS) that builds on an earlier simple model (the RIN), and automates the inclusion of factors that appear to affect eagle range use, especially terrain and ridge features (Chalmers 1998). The model is called the PAT (Predicting Aquila Territory). Golden eagles in Scotland are typically birds of open mountainous country, but exploit a wide range of habitats and landscapes and display a wide range of breeding densities that probably affect ranging behaviour (McGrady 1997, Watson 1997). For a model to predict range use successfully it is important that local or regional variation in ranging behaviour is incorporated. Hence, we outline the derivation of PAT model rules by assessing observed ranging behaviour in relation to geospatial factors in two contrasting areas of western Scotland: an inland, mountainous region and a low-lying peninsula that included coastal ranges. Finally we assess how well the model predicts eagle ranging by comparing its performance against observations of range use in the two study areas of western Scotland and a third study area in southwestern Scotland, and we also compare its performance to that of the RIN model. This exercise highlights the PAT model's strengths and weaknesses, thereby pointing to potential improvements and need for further data requirements.

Methods

Modelling eagle range use and the RIN model

When many observations of eagle range use are available, home range can be estimated using a variety of methods, such as minimum convex polygons, or harmonic mean or kernel estimators (e.g. Kenward 2000). In most situations, however, detailed observations of use are not available and home range must be estimated by other methods. Our objective was to derive a model that could produce an estimate of home range use in golden eagles using only information on eagle nest site location. The model that we developed and describe here, the PAT, is based on an earlier model, known as the RIN (named after the Research and Information Note series in which it was first published; McGrady et al. 1997). It is helpful to understand how the PAT model was developed by briefly describing its precursor's origins.

The simplest method of representing the home range of a golden eagle is to assume it lies within a fixed-radius circle around a nest area, or a range centre, which is the mean location of alternative nest sites (e.g. Watson 1992, Kochert et al. 1999, Pedrini & Sergio 2001a). A more sophisticated method of defining ranges involves Dirichlet tessellation and the production of Thiessen polygons (e.g. Sim et al. 2001). In this method straight lines are drawn mid-way between neighbouring range centres to produce a series of polygons (known as Thiessen polygons) whereby each range contains all the space that is closer to its range centre than to any other. This method has an advantage over simple circles in that it is responsive to differences in nesting density and does not produce any overlap in estimated range use (for more details see Diggle 1983).

As in simpler methods, the RIN model estimates the home ranges of golden eagles in Scotland by first taking the range or territory 'centres' for a group of ranges (described by mean location of recently used nest sites, weighted for use) and drawing up range boundaries equidistant between range centres. For ranges surrounded by near neighbours, a Thiessen polygon results, as in Dirichlet tessellation, but in the absence of near-neighbouring ranges a cut-off of 6 km from the range centre is used to estimate the range boundary (distance based on observations of range use in Argyll, west Scotland). This distance may vary according to the density of breeding eagles and, for example, is likely to be less than 6 km in high density areas such as some of the Hebridean islands (Green 1996). Within the resulting polygon a 'core area', within which 50 % of eagle activity occurs can be delimited by a circle of 2–3 km radius. Outside of the core area it is assumed that eagles do not use land below an elevation threshold of 150 m a.s.l. although this is likely to be lower in the western Hebridean islands and higher in the eastern Highlands (McGrady et al. 1997).

This approach has its advantages, as it is easy to apply in cases when a home range needs to be modelled simply (McGrady et al. 1997, McLeod et al. 2002). However, in all cases so far examined, the RIN model predicts that eagles use larger areas than implied by range use observations (Whitfield et al. 2001, McLeod et al. 2002). The objective of the PAT modelling process was to improve the fit of predicted range use.

Study areas

To derive the rules necessary to generate the PAT model's range use predictions we used range use observations from two study areas in mid and south Argyll in the southwest Highlands and the island of Mull in the Inner Hebrides, respectively (Fig. 1). The mid and south Argyll study area (hereafter called mainland Argyll) was typical of upland sites in the western Highlands of Scotland, consisting of hills, rugged topography and sharp relief in terrain features (< 1100 m, average 230 m a.s.l.; McGrady et al. 1997). The other area was the Ross of Mull, a low altitude (< 400 m, average 100 m a.s.l.) peninsula with gently sloping topography in the southwest of the island of Mull (Fielding & Haworth 1995). Information on nest site use and breeding success of golden eagles was collected in both areas (Green 1996, Whitfield et al. 2001).

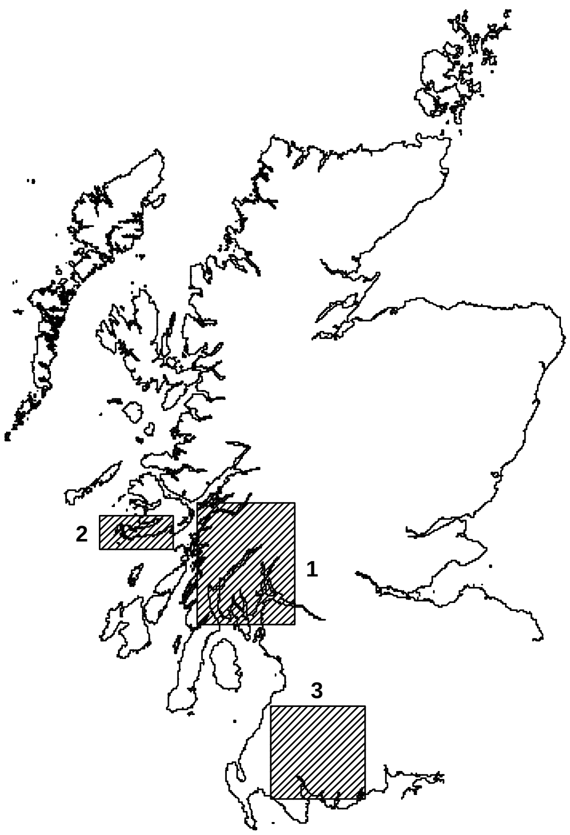

Figure 1. Golden eagle study areas: 1. mainland Argyll, 2. Ross of Mull, 3. Galloway. Individual ranges are not illustrated to retain confidentiality.

Range use observations

Range use data were obtained from two independent studies and combined for the development of the PAT model. We included all observations of range use, collected year-round, to incorporate variations in range use according to season and the breeding status of eagle pairs (Marzluff et al. 1997, P. Haworth & M. McGrady unpublished data). We also used these data to test the fit of the model's predictions. Because these studies initially addressed different objectives there were methodological differences between studies in the data collection methods. The differences in data collection required different methods of data analysis but reduced the risk that our conclusions and the predictions of the PAT model resulted from a methodological bias.

In mainland Argyll, from July 1991 to April 1996, nine adult golden eagles were captured and radio-tracked in six home ranges (details in McGrady & Grant 1996, McGrady et al 1997, Grant & McGrady 1999). In most cases radios allowed two field observers to locate eagles visually and map their movements using a 1 : 25 000 scale Ordnance Survey map. Tracking usually occurred on one home range per day, but this could change to avoid conflicts with hunters and farmers. The main objective of a day's tracking was to get at least one high quality location of a tagged eagle (a high quality location was the visual confirmation of a location at < 100 m accuracy). On most days more than one high quality record was collected and records were later sorted to promote independence of locations (McGrady et al. 1997, McLeod et al. 2002). Eagles were tracked throughout the year, at all times of the day and in all types of weather. If both birds in a pair were tagged the records were pooled (see also Marzluff et al. 1997) so that there was a set of records from each of the six ranges. Strict random sampling protocols could not be followed because access to the home ranges was limited, but our subjective assessment was that because of the large number of observations that were collected this had little effect on estimated range use.

On Mull, observations of golden eagle location and behaviour were obtained as part of a larger long-term study of the Ross of Mull raptor and scavenging bird assemblage (Fielding & Haworth 1995). Because this study was concerned with many individual birds in a raptor community, radio tracking of individuals was considered impractical. Observational records (n = 1895) of eagles were gathered in an area encompassing five ranges, by two experienced field workers who were on occasion supported by volunteers, between August 1994 and December 1998 inclusive. Random sampling was not possible because of access and safety constraints. Sampling effort was greatest, and approximately constant, throughout daylight hours, between July and October. Observations were collected using binoculars and spotting telescopes and mapped onto 1 : 25 000 maps of the study area. Birds were aged (Tjernberg 1988) and, if possible, sexed on size. Only records of territory holding adults were used in analysis (n = 1382), although we could not identify adult intruders. As in mainland Argyll, records for both sexes were combined for each range. If an observation could not be unambiguously assigned to a particular range it was assigned to the range whose nest was closest to the location of the record. Because eagles on Mull were not fitted with radio tags serial dependence of records was not a potential problem. For this reason, and because we did not wish to compromise sample sizes (Reynolds & Laundre 1990, De Solla et al. 1999, Otis & White 1999, Seaman et al. 1999), all observations from this study area were used in the range modelling procedure.

The lack of random sampling within the Ross of Mull study area meant that the observations were potentially biased and not representative of actual range use. We addressed this by expressing golden eagle records in an area relative to the records of other raptor and scavenging species, as follows.

The 1382 observations of adult golden eagles comprised 7.2 % of all sightings of raptors and scavengers (n = 19291 observations on 14 species). Within the GIS a simple kernel estimator (using a circular buffer, 250 m radius) was applied to each 50 × 50 m pixel in the Ross of Mull study area (Bailey & Gatrell 1995). In each buffer the proportion of adult golden eagle sightings was calculated, with 95 % confidence limits (Agresti & Coull 1998), as a proportion of all raptor sightings within the buffer. If the lower confidence limit was greater than 0.072 (the overall proportion of sightings that were adult golden eagles) this was taken to indicate excess usage, while an upper confidence limit less than 0.072 was indicative of under-use. A small number of buffers had no sightings, either because none of the 14 species had been seen or the location was rarely visited. In all other locations usage did not differ from the expected proportion. Although this method probably did not wholly resolve the problem of potential sampling bias, it was an improvement as the number of raptor sightings was large and it was probably best for identification of those areas seldom used by eagles. The method did not depend on the correct allocation of golden eagle sightings to ranges. It also dealt with inequalities in sampling effort because rarely visited locations had wide confidence intervals. We could be confident about under-used locations because buffers typically had many observations from other species. The output from these analyses was an indicative 'preference' map in which each 50 × 50 m pixel was assigned to one of four possible values: over-used, under-used, proportional (observed = expected) use, no data.

Predictive models are only of value if their predictions are tested on independent data, i.e. data that were not used during the model's development (Fielding & Bell 1997). Fortunately, we were able to obtain range use observations from two golden eagle ranges in Galloway, southwest Scotland, collected under a third independent study; hence the method of data collection differed from the studies on Argyll and Mull. These ranges are isolated from the main golden eagle Scottish breeding area in the Highlands (Fig. 1). Marquiss et al. (1985) and Watson (1997) have provided descriptions of the area and study ranges. The area within 10 km of eyries was divided into 1 × 1 km grid squares according to the Ordnance Survey national grid. Several experienced volunteer observers visited the area between 1987 and 1991 in the course of keeping the eagles under protective surveillance and to estimate the use of the region by eagles. The number of observations of eagles in each grid square was recorded along with the number of times each grid square was visited by an observer. The relative use of each grid square was expressed as the proportion of visits when an eagle was seen. The relatively coarse scale of analysis was chosen to accommodate the relatively coarse scale at which many observations were made. Visits were not timed but approximately equal times were spent in each grid square. While emphasis was on collecting observations of adult birds, the age of eagles was not recorded in every case and this may have biased records, especially on the periphery of ranges (Watson 1997). If an observation could not be unambiguously assigned to a particular range it was assigned to the range whose nest was closest to the location of the record. The isolation of the ranges, however, meant that such observations were few.

Golden eagle habitat requirements: model assumptions

Our first assumption was that eagles used exclusive ranges with no overlap between neighbours. Although it is apparent that there can be overlap in range use between neighbours (Marzluff et al. 1997, this study), there is good evidence for active defence of an area at least at some times of the year (reviewed by McGrady 1997, Watson 1997). It is also simpler to model exclusive ranges.

Eagles also appear to use areas around their nest sites more frequently than other parts of their range. To a degree this is probably because eagles are central place foragers during the breeding season, but the preference is also apparent when eagles are not breeding (McGrady et al. 1997, Marzluff et al. 1997, this study). As nest site locations are often used to define the 'range centre' (e.g. Watson 1992, Kochert et al. 1999, Pedrini & Sergio 2001a), an area around the range centre so defined should be a preferred area.

Golden eagle morphology is adapted for soaring flight (McGrady 1997, Watson 1997), and so features of the terrain that aid soaring flight may affect range use. In the cool climate of Scotland wind deflected upward off terrain features is probably an important aid for flight. In keeping with this suggestion, Chalmers (1998) found a statistically significant association between eagle activity and ridge features (see also Orloff & Flannery 1996, Erickson et al. 1999, Strickland et al. 2000). We therefore assumed that ridges and similar terrain features would be preferred by eagles.

Golden eagles are sensitive to disturbance by humans and tend to avoid areas of human activity, such as settlements and roads (e.g. Anderson et al. 1990, Watson 1997, Petty 1998). There is little quantified information, however, on the distances at which disturbance can occur or which activities are most affected. Throughout their global range, eagle tolerance of human activities varies, and in recent years eagles in an expanding population have moved into areas more disturbed by humans to establish new breeding ranges (Haller 1996). As such a situation is not apparent in Scotland (Watson & Dennis 1992) we assumed that areas of human activity would be avoided by eagles.

Water bodies and the sea provide few air currents that golden eagles can exploit, and provide few prey sources (Watson 1997): they were therefore treated as areas that golden eagles did not use. Golden eagles in Scotland also seldom exploit post-thicket (closed canopy) forests (Marquiss et al. 1985, Watson et al. 1987, Watson 1992, McGrady et al. 1997, 2001, Whitfield et al. 2001). Hence, we assumed that golden eagles did not use forests more than twelve years old, since field observations determined that this was the age when forests became unavailable to them (Whitfield et al. 2001). Golden eagles appear to use particular vegetation types more than others (Marzluff et al. 1997, McGrady et al. 2001). We did not attempt to incorporate any vegetation preferences within the PAT model, however, because across Scotland prey selection differs (Watson 1997) and so vegetation preferences probably also differ, making their incorporation in a generic model difficult.

The GIS, model rule-base and model development

All modelling was undertaken in a raster digital GIS using ArcView® (ESRI). The principal source of terrain data was the Ordnance Survey's (OS) 1 : 50000 raster digital elevation model. As the OS digital elevation data has a pixel size of 50 × 50 m, terrain features of less than this area could not therefore be identified. Nevertheless, we deemed prediction to this scale as appropriate both to the accuracy of range use observations and to how eagles may select areas within their range. Road and human settlement data came from OS. Water bodies (not including rivers and streams) were derived from the Land Cover of Scotland 1988 (LCS88) dataset (MLURI 1993). Whitfield et al. (2001) described the methods by which post-thicket forests were mapped in the GIS.

As a first step in the model we estimated the range centre as the mean position of used nest sites, up to a

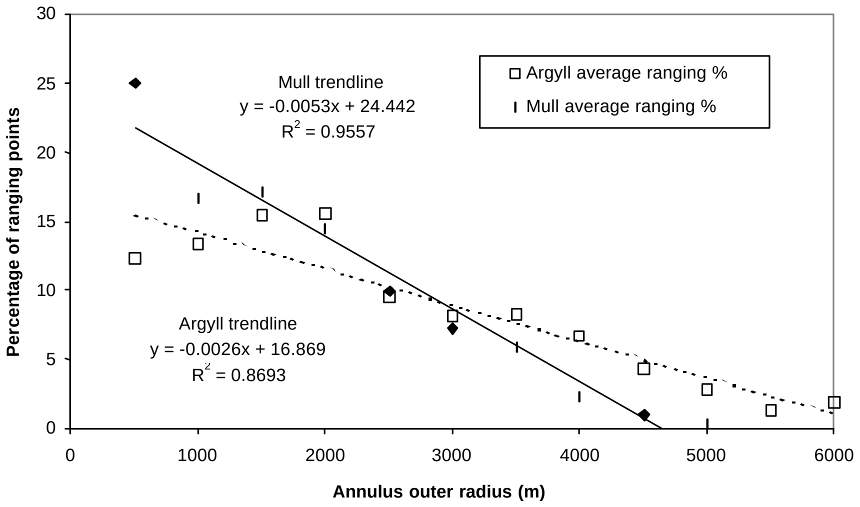

Figure 2. Relationship between distance from the range centre and mean percentage ranging observations for golden eagle ranges on Mull (n = 5) and mainland Argyll (n = 6).

maximum of the previous ten years usage (see also McGrady et al. 1997, Kochert et al. 1999, McLeod et al. 2002). If a minimum of five years information on nest use was not available, then we used the mean position of known alternate nests. Next, range boundaries were estimated by drawing lines at the equi-distant points between neighbouring range centres (Dirichlet tessellation) to produce Thiessen polygons. In the absence of neighbours or unsuitable habitat we set the boundary of a range at 6 km (see McGrady et al. 1997, McLeod et al. 2002), but we took this as a preliminary measure only, because it was inflexible (see later). Thus far, the model was the same as earlier approaches, including the RIN, and had incorporated the assumption that ranges were exclusive.

The next step was to incorporate a preference for use of areas around nest sites (i.e. the range centre). Concentric annuli, in 500 m width increments, were drawn around the centre of each range (i.e. annulus 1 = 500 m radius, annulus 2 = 1000 m radius, etc.) to form concentric distance bands (i.e. band 1 = 0–500 m, band 2 = 500–1000 m, etc.). Our approach was to assume that eagles' use of areas would be greater within annuli closer to the range centre, and we used the range use observations from mainland Argyll and Mull to derive the rules for how much 'use' should be assigned to (= predicted to occur within) each distance band. We took the complete use of an eagle range to be 100 %, so that each pixel within a range had a use value (the percentage of total range use the model predicted for that 50 × 50 m tile) and the sum of all pixel use values was 100.

Ranging observations, measured for Euclidean distance to the range centre and assigned to the appropriate distance band, were aggregated for all ranges within each study area. For each study area we plotted the percentage frequency of ranging observations against distance class (Fig. 2). This confirmed that eagles preferred areas close to the range centre. But it was clear that since ranges were markedly different in size, it was necessary to know the maximum ranging distance (as a measure of range size) in order to assign use values to the different 500 m distance bands. In other words, if we could estimate the maximum ranging distance (the *x* intercept) then from the relationship we could predict the slope (how range use changed with distance from the centre).

The best estimator for maximum ranging distance in a range was found to be the area of the Thiessen polygon for that range (Fig. 3). The reason why a measure of area was a good surrogate for a measure of distance (Fig. 3) was probably that both were influenced by the same features (breeding density and the presence of unsuitable habitat constraining range use). Estimation of maximum ranging distance in turn allowed, for any range, the estimation of the slope of the relationship between percentage ranging observations and distance (Fig. 2), and thus the percentage of range use per distance band (the use value assigned to each 500 m distance band). We also assumed, therefore, a linear decrease in range use occurred between 500 m distance bands with distance from the range centre, as determined by the empirical relationship (Fig. 2).

As noted earlier, although we had set the maximum ranging distance at 6 km we had taken this as a preliminary measure only, since it was apparent that in areas of high density (such as on Mull) golden eagles typically did not range as far as 6 km from the range centre. We therefore needed to set maximum ranging distance by a means that was responsive to local breeding density. Deriving a surrogate for maximum ranging distance (using the relationship in Fig. 3) allowed us to estimate the limit for range boundaries in areas where neighbouring ranges were absent. Dirichlet tessellation and Thiessen polygons delineated range boundaries in the presence of near neighbours, as described earlier, but in the absence of near neighbours we assumed that the boundary of an eagle range occurred at the maximum ranging distance from the range centre, estimated according to the relationship in Figure 3. Thus boundaries unconstrained by near neighbours were described by a distance responsive to local breeding eagle density in the PAT model rather than by a fixed 6 km distance as in the RIN model (McGrady et al. 1997). This reflected the observation that eagles whose near neighbours were closer also ranged shorter maximum distances in parts of the range unconstrained by neighbours.

The next stage of the model's development was to incorporate eagles' preference for ridge features. This first required us to use a method for recognising ridge and cliff/plateau edges (i.e. convex terrain features). None of the facilities within ArcView (e.g. watershed or curvature functions) were found to be suitable for our purposes. Instead, using a custom script (a small program written in Avenue, Arcview's programming language), terrain features were automatically detected by comparing the altitude of each pixel with those of its neighbours (McLeod et al. 2002).

The altitude of each pixel was compared to the mean elevation of four opposing pairs of radial arms, each arm five pixels in length, which were orientated NE-SW, N-S, SE-NW, and E-W (the method is illustrated by McLeod et al. 2002). From the elevation values we calculated the angle formed by each pair of opposing radial arms about the 'focal' pixel. If the angle between any pair of radial arms was less than 168° we deemed the focal pixel to be a 'convex terrain feature'. The threshold value for the angle was largely dictated by pixel size but was chosen subjectively because it provided the best fit to features we thought likely to be used by eagles. Although we did not distinguish between cliff/plateau edges and ridges, ridges may be distinguished by this method if all pixels on a pair of opposing radial arms were lower than the focal pixel. This process was carried out on every pixel with-

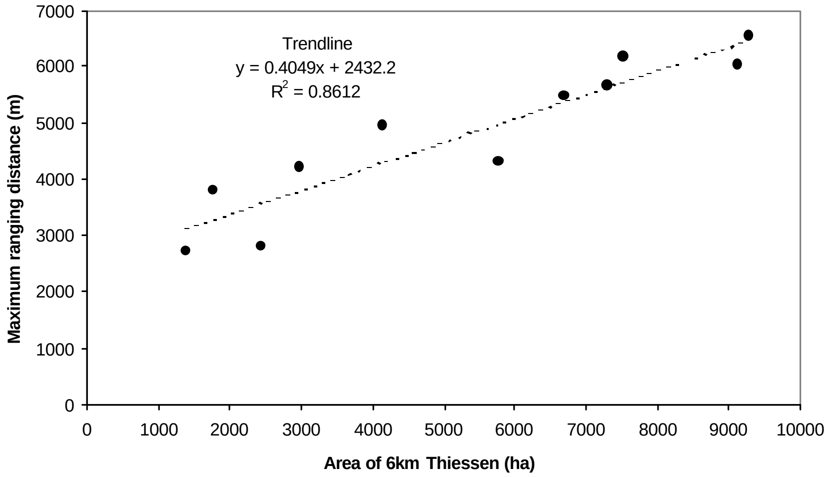

Figure 3. Relationship between maximum ranging distance and the area of a Thiessen polygon, limited to a maximum of 6 km from the range centre in the absence of neighbouring ranges, for the 11 golden eagle study ranges in mainland Argyll and Mull. The peripheral area of a home range where maximum ranging distances were recorded had the fewest empirical data (a general finding: see Seaman et al. 1999) and this may lead to errors in the measurement of home range area and maximum ranging distance. Consequently, values for maximum ranging distance in each study home range were estimated by linear extrapolations from 90 % values taken from a plot of percentage ranging observations against distance from the range centre.

in the maximum ranging distance from the range centre.

To obtain the rule for how use values should be distributed according to terrain features, we drew up incremental 100 m wide distance bands from all convex terrain features in the two study areas up to a maximum of 1200 m distance, as almost every point in a home range was within 1200 m of a convex terrain feature. We then measured all range use observations from both study areas for Euclidean distance to a convex terrain feature, and assigned each observation to the appropriate distance band. Ranging locations of eagles were more frequent within 200 m of a convex terrain feature than would be expected if they were evenly distributed within a 1200 m distance from convex terrain features, confirming that convex terrain features were preferred by eagles (Fig. 4). This relationship gave us the rule for assigning use to each pixel according to distance from convex terrain features.

This rule was incorporated in the model so that within each 500 m wide annulus from the centre, we assumed that range use was distributed between 100 m terrain distance bands according to the observed distribution relative to convex terrain features in Figure 4 (i.e. use was greater closer to convex terrain features). So, for example, if the use value assigned to an annulus around the centre was 30 (%) then the relationship in Figure 4 and the number of pixels in the annulus dictated how the 30 'percentage points' were distributed between pixels across terrain distance bands.

The next set of rules, for eagles' avoidance of areas with human activity and unsuitable habitat, were easier to implement, since the relevant features were simply excluded. In the absence of specific information, buffer zones around human settlements, within which eagles were assumed not to range, were created as follows: single building 250 m, cluster of buildings 400 m, village 600 m, and town 800 m. These distances were based on limited observations of ranging behaviour within the study areas and experience of golden eagles elsewhere in Scotland. Roads are more difficult to buffer, as it is unlikely that traffic volume can be reliably related to road category (especially in the Scottish Highlands). It is not the presence or proximity of the road per se that may affect eagle ranging, but its visibility and traffic volume (Andrew & Mosher 1982, Gonzalez et al. 1992). However, as a simplistic representation, we assumed that eagles did not use areas within 300 m of single carriageway roads and within 500 m of dual carriageway roads.

We also assumed that eagles did not use freshwater bodies (i.e. pixels overlying freshwater had no use value), with no minimum size for exclusion. The sea was excluded by assuming pixels seaward of the coastline in the OS data had no use value. Pixels that overlaid woodland that was over 12 years old in the forest layer of the GIS were also taken to have no use value, because we assumed eagles also avoided this habitat

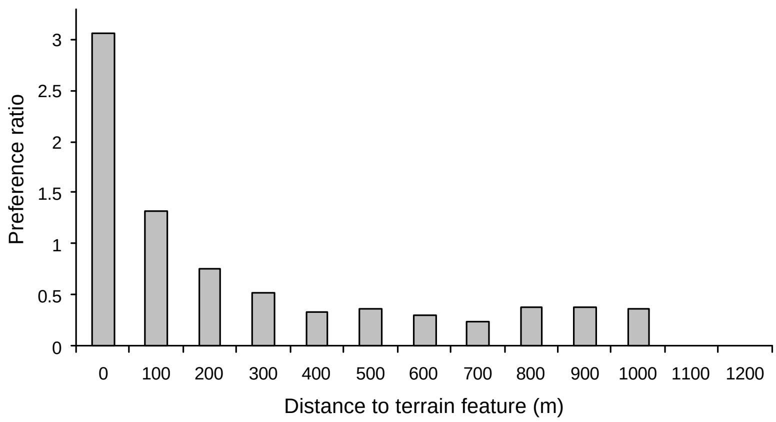

Figure 4. The relationship between distance from a terrain feature (ridge or convex feature) within 100 m wide distance bands and the 'preference ratio' of golden eagle range use (observed range use/expected range use). Expected range use was the availability of land within each distance band. The zero distance class represented ranging over a terrain feature. Eagles were observed more often close to terrain features than expected from the availability of land (11 distance bands, Kolmogorov-Smirnov two-sample test, D = 0.64, P = 0.02, two-tailed).

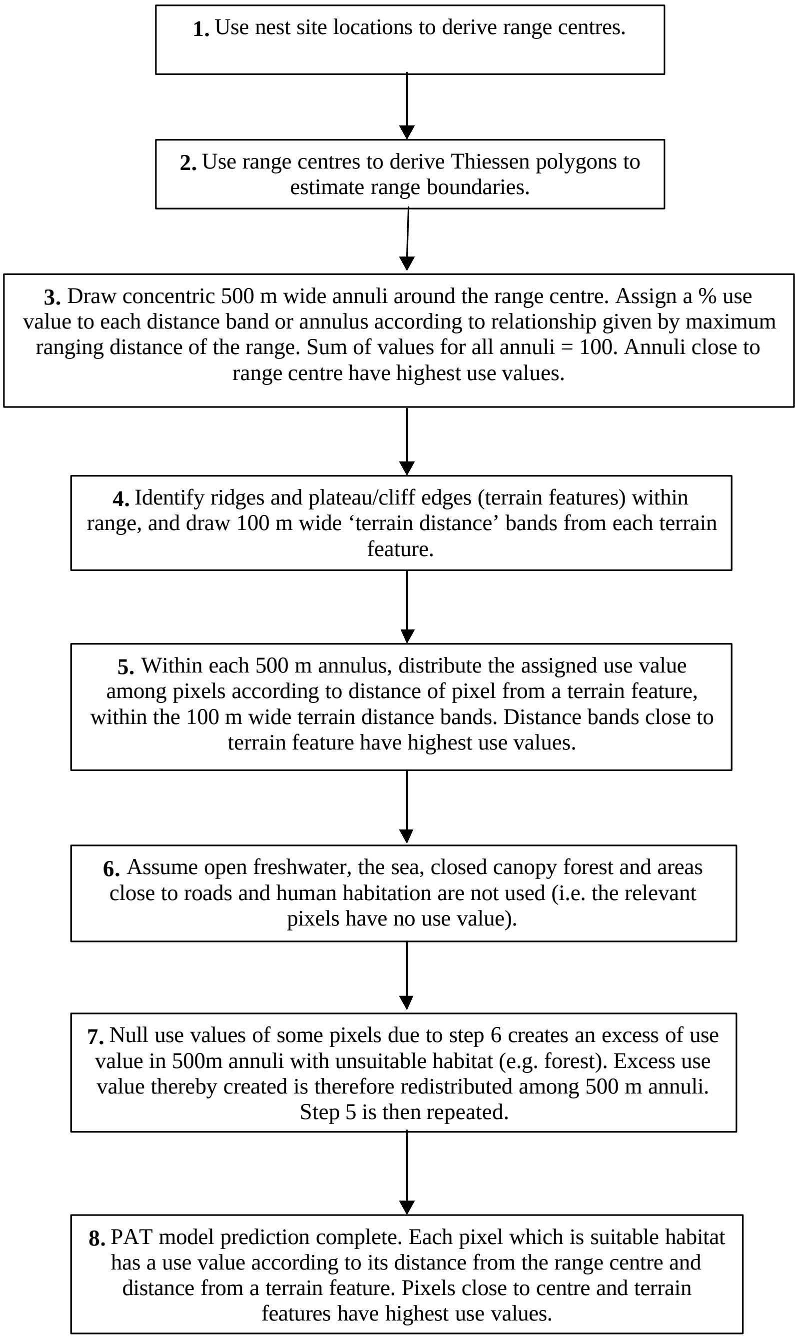

Figure 5. Flow chart summarising the steps in the prediction of range use by golden eagles using the PAT model.

Accounting for shifts in range use and final model output

Creating pixels with no use value due to unsuitable habitat (water, closed canopy forest, road buffers, human settlement buffers) was akin to introducing habitat loss to a range. If eagles are prevented from using an area then their proportional use of other areas is altered (Kochert et al. 1999, Whitfield et al. 2001). Hence this shift in range use needed to be incorporated within the PAT model.

We do not know exactly how eagles respond to habitat loss and so to account for such alterations we used a subjective rule. The foundation of this rule was that any reduction in the area within a 500 m distance band caused by an exclusion area, resulted in a proportional over prediction of range use in that distance band. This means that, for example, if a distance band has 500 pixels and has been assigned a use value of 16 % then each pixel represents, on average, 16/500 = 0.032 % of predicted range use. If, however, 250 of the pixels are closed canopy forest then each pixel represents, on average, 16/250 = 0.064 % of range use, so that simply because much of the distance band is unsuitable habitat this inflates the predicted proportional use for the remaining pixels of suitable habitat in that distance band. It seems very unlikely that eagles would compensate for the loss of habitat only by increasing their use of areas immediately surrounding the lost area, so there was therefore a need to spread the excess of predicted range use within and between the 500 m wide distance bands.

The subjective rule underpinning this redistribution was that 25 % of the excess was retained in the source distance band (where the unsuitable habitat or exclusion area was located), 25 % was shifted towards the range centre in the adjoining distance band, 25 % was shifted away from the centre by one distance band, and 25 % was shifted away from the centre by two distance bands. For an exclusion area in the central distance band or in the outer distance band, excess predicted range use was redistributed equally throughout all other distance bands. In addition, each distance band was restricted to a maximum predicted range use per unit area (based on the observed maximum for eagle ranges in the region): any excess was redistributed using the 25 % rule. Thus for distance band x, expected to contain 16 % of the total predicted range use, but which had its area reduced by 0.5 through the presence of an exclusion area, 2 % (25 % of (0.5 × 16)) of the predicted range use was shifted to the neighbouring distance band $x - 1$ (i.e. towards the centre), 10 (8 + 2) % was retained in band x, 2 % was shifted out to band $x + 1$, and 2 % was shifted out to band $x + 2$. Having redistributed predicted range use between distance bands because of excluded features, it was then redistributed within distance bands based on the separate preference rules for being near or over terrain features, as described earlier.

This was the last stage in the modelling process (Fig. 5). Following incorporation of all variables, the PAT model output was a raster representation of predicted range use, each 50 × 50 m pixel having a predicted 'use value'. For each range, the sum of these use values was 100, with the value of each pixel being a percentage of the sum of the values of all pixels. Pixels with higher use values were located near the range centre and around terrain features, and pixels with the lowest values were further away from the centre and terrain features (Fig. 6).

Model evaluation

As noted earlier, due to differences between study areas in data collection methods we had to employ different methods of analysis. For each study range on mainland

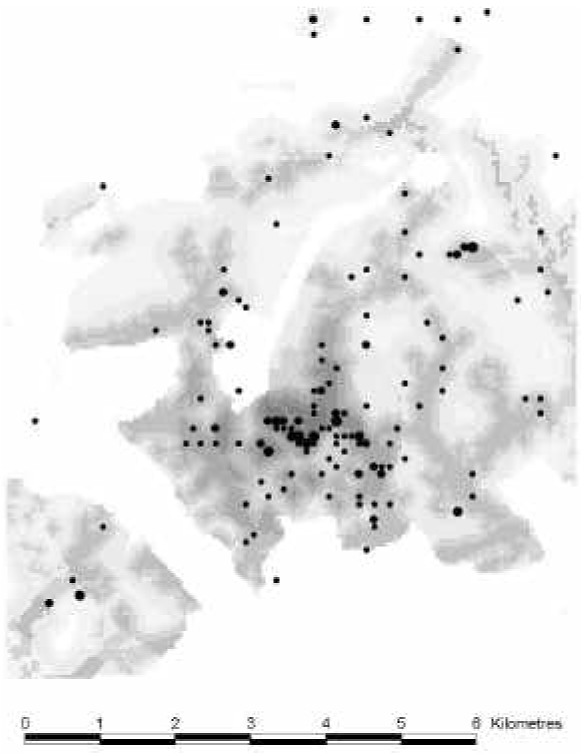

Figure 6. Two dimensional representation of predicted range use for a golden eagle territory according to the PAT model (shaded areas) and observations of actual range use (solid circles – size proportional to number of observations) for a study range in mainland Argyll. For the PAT predictions different intensities of shading represent different classes of predicted range use with darker shading representing greater predicted use of an area (number of classes kept low in this example for clarity of presentation). Note also that range use observations are not necessary to generate the PAT predictions, but in this case the PAT model was run for a study range to give an indication of 'observed' use.

Argyll and Mull the fit of the observed data to the PAT predictions was examined first using quantile-quantile or Q-Q plots. Q-Q plots compare observed and expected quantile values drawn from frequency distributions. If the observed data fit the expected data perfectly the points form a straight line (see Sokal & Rohlf 1995 for details). Expected quantiles were taken from the PAT model's frequency distribution of predicted range use relative to the range centre and the observed quantiles were taken from the frequency distribution of actual range use observations with distance from the range centre. The number of data points varied between ranges because ties were removed. The fit of the observed data to the PAT model was also tested using a Kolmogorov-Smirnov goodness of fit test ($\alpha = 0.05$): data were assigned to 20 classes (5 % increments) of distance from the range centre.

The predicted utilisation surface from the PAT model for the Ross of Mull was overlaid on the preference map within a GIS. To facilitate the overlay operations and comparison of layers, PAT-predicted usage values in each pixel were classified into 8 bins with equal increments and tabulated against the corresponding preference class. Only pixels predicted as having a usage value by the PAT model were included in the analyses. Frequency distributions and mean values of the PAT usage predictions were compared for three of the four preference classes (the no-data class was excluded).

We also tested the model against range use observations collected on two ranges in Galloway. The PAT model was run for the two Galloway ranges values based on a range centre calculated from the nest sites used over the observation period and we summed the predicted use for all pixels within each 1 km OS grid square that was visited by observers. We then entered these values in a linear regression against the observed values of use (proportion of visits by an observer to the grid square when an eagle was seen) for the same grid squares. Each range was analysed separately, and any grid squares with no visits were excluded because these grid squares were always some distance from the range centre and would be predicted to be little used by the PAT model. Inclusion of such squares would have introduced a spurious positive relationship between no 'observed use' and low predicted use.

To test whether the PAT model was more 'efficient' than the RIN model we examined whether, in the 11 mainland Argyll and Mull home ranges, it predicted smaller areas for the same percentage of observed range use points. In each range for each model we calculated the area that was predicted in order to encompass the same 50 % of the observed range use points. The RIN model was run with an assumed 2.5 km 'core area' and with a 6 km cut-off from the range centre in the absence of a neighbouring range.

Results

Model output

The PAT produced an output with three dimensions: the geographic location as *x* and *y* co-ordinates and predicted range use as a percentage of the total use as a *z* co-ordinate. Resolution was to 50 × 50 m (equivalent) pixels, each pixel with a predicted percent use value (Fig. 6).

We generated a 'use surface' by ranking the pixels in descending order according to their individual percentage use value, and then cumulatively summing the use values until notional percentages of total range use were reached. Isolines could then be drawn around all pixels that contributed to each notional percentage of total range use. For example, the 80 % isoline encompassed all of the pixels with the highest use values that summed to 80 %, and represented the geographic area required to encompass 80 % of the predicted ranging of an eagle pair. Other methods, such as a kernel estimator can only derive such a 'density surface' when there are observations of eagle range use. The PAT model generates a density surface using only information on nest site locations.

Model evaluation

The Q-Q plots indicated that there was no consistent bias in the PAT model's predictions of range use for the 11 ranges on mainland Argyll and Mull (Fig. 7). Under-prediction occurred when the PAT predicted that the eagles used areas closer to the range centre more frequently than was observed. Under-prediction may have occurred on some ranges because they were more successful for breeding and so parents spent more time around the nest (range centre). On Mull three range use distributions were under-predicted by the PAT, and two range use distributions were over-predicted. Qualitati-

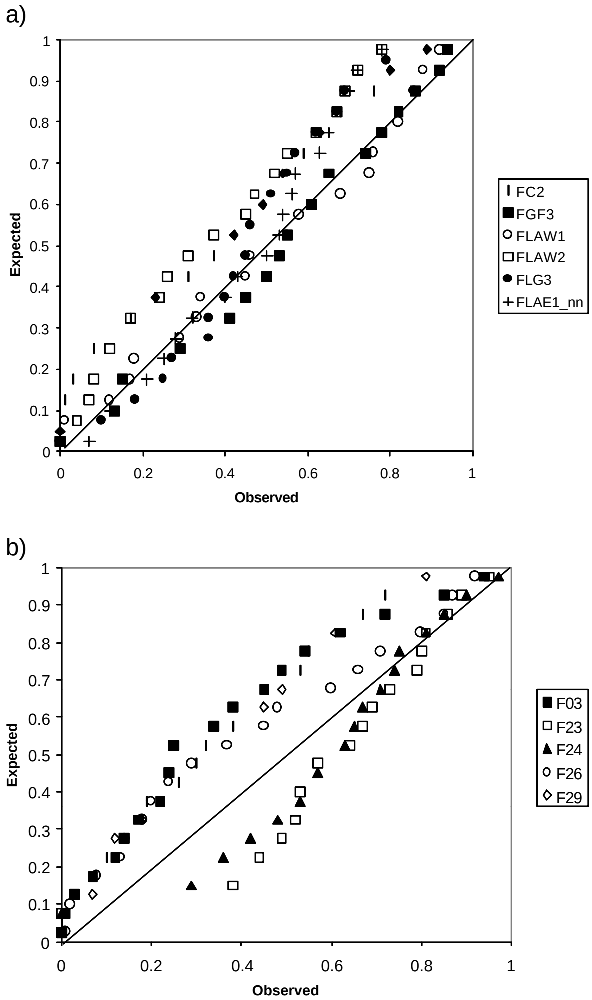

Figure 7. The observed and expected (= predicted by the PAT model) distributions of ranging points with distance from range centre plotted as Q-Q plots for a) six golden eagle home ranges on mainland Argyll and b) five home ranges on Mull. Deviations from the line represent deviations from a perfect relationship between observed and expected. The legend identifies codes for individual ranges.

vely, predictions of the PAT for the mainland Argyll ranges appeared to show a better fit, with a tendency to over-predict. Two of the three under-predicted ranges on Mull were neighbours and had nest sites on high sea cliffs and one of these was highlighted for a lack of fit using the Kolmogorov-Smirnov tests (Table 1). There was no significant difference, however, between PAT-predicted and observed distributions of range use in any of the other ten ranges, suggesting that overall the PAT provided good estimations of observed range use. The range on Mull with one of the poorest fits of predicted use to observed use had two alternative nest sites 2 km apart that were both used in the study period. Historically (30 years ago) these two alternatives were two ranges but in the last 10 years we are certain that the area has been used by only one pair. A better fit would probably have been obtained if the range had been considered as having two range centres (for split range centres see also McGrady et al. 1997). Prior to analysis, however, we could not justify this split, despite the range's history, because other ranges on mainland Argyll had alternative nest sites as far apart as this Mull range.

One-way ANOVAs indicated that for each of the five Mull ranges the predictions of use by the PAT and the usage preference classes were strongly associated (Table 2). This was a further confirmation that the PAT predictions of range usage were a good fit to the empirically derived estimates of range usage.

For the two ranges in Galloway there was a significant positive relationship between the observed use and PAT-predicted use (range DG1: n = 130 grid squares, t = 7.47, R^2 (adj) = 0.30, $P < 0.001$; range DG3: n = 129 grid squares, t = 7.85, R^2 (adj) = 0.31, $P < 0.001$). Removal of one strong outlier in the DG1 regression improved the relationship markedly (t = 11.54, R^2 (adj) = 0.51, $P < 0.001$). Weighting the observed values to account for differences in the number of visits between squares had little effect on either the slope or R^2-value of the relationships.

For all 11 ranges in mainland Argyll and Mull the RIN model predicted a larger area than the PAT model to encompass the same 50 % of range use observations (median & range, ha: RIN, 950 & 100–1830; PAT, 730 & 75–1080; Wilcoxon test, Z = 2.93, P = 0.003). As the percentage of range use observations increased, the area predicted by each model to encompass the observations also increased, but the difference between the models in the predicted area increased too. This was expected given that the RIN is very coarse when including areas as part of a predicted home range whereas the PAT is much more specific and, therefore, efficient.

Discussion

Kolmogorov-Smirnov tests are especially sensitive to small differences in distributions (Syrjala 1996), so

Table 1. Results of Kolmogorov-Smirnov two-sample tests of differences in frequency distributions of golden eagle range use relative to range centre for PAT predictions and field observations for 11 home ranges on the Ross of Mull and mainland Argyll. The term D is the largest unsigned difference. * $P < 0.05$, two-tailed.

Home range	D
ML03	0.28
ML23	0.30*
ML24	0.20
ML26	0.20
ML29	0.17
C2	0.20
LG3	0.13
GF3	0.17
LAE1A	0.16
LAW1	0.14
LAW2	0.21
All ranges	0.05

the lack of a significant difference between observed and PAT-predicted distributions for most of the study ranges suggests the model was robust. The Q-Q plots indicated that there were no systematic biases in the model predictions. Testing the model against the same data used in its derivation, nevertheless, was not the best test of the model (e.g. Wiens 1989). The better tests of the PAT, however, for two ranges in Galloway that were not used in the model's derivation, also pointed to a reasonably robust predictive capability. Despite the coarseness of the scale of the observations relative to the PAT's predictions and the isolation of Galloway golden eagles, which may have produced unusual range use behaviour, there was a good agreement between observed and predicted use patterns.

Although the PAT appears to produce robust predictions, improvements can be made, possibly including the alteration to range use where the centre is close to a boundary (e.g. when pairs nest on sea cliffs), accounting for split range centres, and accounting for the possibility that golden eagles use terrain features as territorial boundaries. To make such improvements will require further observations of golden eagle ranging. Observations of golden eagle range use elsewhere would also test the utility of the PAT in environments different to western Scotland. The modelling approach may also be worth considering for other raptor species that have similar ecology to golden eagles.

The PAT is a novel approach to modelling golden eagle range use but most features it incorporates have been described by previous studies (see Methods). Relatively few vegetation features were used to predict range use, although golden eagles can exhibit preferences for particular vegetation types that are associated with preferred prey (Marzluff et al. 1997, Pedrini & Sergio 2002), or avoid habitats that are structurally unsuitable for foraging (e.g. Watson 1992, Pedrini & Sergio 2001a, Whitfield et al. 2001). Incorporation of vegetation characteristics would probably improve the predictive ability of the PAT, especially if prey is strongly tied to vegetation that is distributed heterogeneously. Prey in the two study areas was markedly different (Watson 1997), however, so it is perhaps surprising that the model has at least reasonable predictive success when terrain is the principal 'habitat' parameter.

While there may be a link between vegetation classes and terrain features, terrain probably mainly acts as a surrogate for wind and air currents. In essence, the predictive success of the PAT strongly suggests that in Scotland wind and air currents are a resource that ea-

Table 2. Results of ANOVAs for the relationship between eight incremental classes of predicted use by the PAT model and three classes of indicative preference (no data class excluded) as observed on five golden eagle ranges on the Ross of Mull. Sample size was the number of pixels (50 × 50 m equivalent) in each range.

Range	Source	df	Sum of squares	F	P	Source	df	Sum of squares
ML24	Preference	2	86806	42.65	<0.001	Error	4814	4899411
ML29	Preference	2	286313	186.70	<0.001	Error	3403	2609339
ML03	Preference	2	419719	426.92	<0.001	Error	8922	4385766
ML23	Preference	2	1239564	393.64	<0.001	Error	4466	7031742
ML26	Preference	2	296038	143.34	<0.001	Error	6985	7212802

gles select and should be considered as a major contributor to 'habitat suitability'. Rugged terrain also probably allows eagles to hunt over a larger area of land per unit time of flight, and may also allow prey to be surprised more easily. In many mountainous regions more rugged areas are also associated with low human disturbance and a low level of development, which are probably favoured by eagles (Watson 1997). Areas associated with thermals, such as patches of scree or rock outcrops, may also be important components of habitat selection, especially in warmer environments. The importance of air currents to large raptors when on migration is well known (e.g. Smith 1985), so their influence on more local movements should not be unexpected, even if rarely considered previously (Bögel & Eberhardt 1997). Future studies of habitat selection for some raptors should move beyond a consideration of habitat only in terms of vegetation. This applies not just to species adapted to soaring flight (Strickland et al. 2000) but to species that predominately use other flight behaviours (Jiménez & Jaksic 1993).

Particular activities, including hunting and territory defence might be associated with certain portions of the range. These might be incorporated into estimates of range use if appropriate data were collected, although for golden eagles it may be difficult to distinguish active hunting from simply flying from one part of a range to another (Watson 1997). Also, some areas may be important only as a connection between areas important for other reasons (Fielding et al. in press). McGrady et al. (1997) pointed out an example of this where a large block of forest may have discouraged use of areas beyond the block's boundaries.

The PAT essentially represents an extension of the RIN, incorporating many features identified by McGrady et al. (1997) as important but not formally included in the RIN. While the PAT probably provides a more accurate prediction of range use (McLeod et al. 2002), the simplicity of the RIN model's implementation should retain its usefulness in many situations. The greater efficiency of the PAT makes it preferable when range use predictions need to be more precise, but its application requires access to supporting software such as digital terrain data and other aspects of a GIS, in contrast to the RIN. On the other hand, ongoing work to improve the RIN should aim to incorporate formally the regional variation in range dimensions that this study has illustrated, especially when considering that regional variation in density, probably related to food availability, is a common feature of golden eagle populations (e.g. McGrady 1997, Watson 1997, Pedrini & Sergio 2001b, 2002). Both the RIN and the PAT require a priori knowledge of the location of nest sites, and in some poorly studied areas this knowledge will not exist. Nevertheless, the effort to locate nest sites is far less than the effort required to document actual range use.

The impact of developments such as wind-farms and forestry can be assessed according to their proposed location in relation to predicted range use. The models can be used to identify boundaries of protection areas for golden eagles and identify locations where management to improve ranges would be most effective. Connection of the range modelling software with a national database on the distribution of eagle nest sites (Green 1996) provides landscape-scale information on areas predicted to be important for breeding eagles (McLeod et al. 2002), and allows for more strategic conservation planning. Marzluff et al. (1997) emphasised the need for managers to take account of variation in golden eagle range use if conservation strategies are to be effective, while Pedrini & Sergio (2002) have highlighted how regional gradients in density, diet composition and productivity may be used to set priorities for golden eagle conservation at the landscape scale.

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