A MODEL OF GOLDEN EAGLE (AQUILA CHRYSAETOS) RANGING BEHAVIOR

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ABSTRACT.—Eight territory-holding adult Golden Eagles (*Aquila chrysaetos*) were radiotracked in all seasons from 1991–96 in western Scotland. Mean territory size was 6827 ha (range = 2604-12.835 ha). Core areas (50% of locations) used by tracked eagles averaged 498 ha. Tracked eagles moved up to 9 km from the center of their territories, but over 98% of observations were <6 km of the center. Loglinear models showed no significant preference for land cover, although relative use suggested the order of preference by eagles to be: montane > heather > coarse grassland > bracken > smooth grassland > bog > broad-leaved forests > pre-thicket forest > post-thicket forest > pasture > other habitats. Elevations ranged from sea level to 900 m but eagles appeared to prefer elevations between 150–549 m. Based on data from these eagles, we constructed a simple model to define likely boundaries of territories and to identify areas within those boundaries that are likely to be important to eagles. Features of the model included range centers identified from nest locations and nest-use data, boundaries with near-neighbors halfway between respective nest centers, and a 6-km cutoff in directions where neighbors were distant. The model designated core areas 2–3 km in radii using information on local eagle nesting density. Outside core areas, low elevations were avoided. We discuss the advantages and shortcomings of the model and its robustness when exported to other parts of Scotland.

KEY WORDS: Golden Eagle; Aquila chrysaetos; range; movements; territoriality; Scotland.

Un modelo del rango de comportamiento del águila real (Aquila chrysaetos)

RESÚMEN.—Nueve águilas reales (Aquila chrysaetos) adultas poseedoras de territorios fueron rastreadas con radios en todas las estaciones desde 1991-96 en el oeste de Escocia. El tamaño medio de los territorios fue 6827 ha (rango = 2604-12835 ha). Las áreas centrales (50% de las localizaciones) usadas por las águilas rastreadas promediaron 498 ha. Las águilas rastreadas se movieron por eucima de 9 km desde el centro de sus territorios, pero mas del 98% de las observaciones estuvieron a <6 km del centro. Dos modelos de Logaritmo linear no mostraron preferencias significativas para la cobertura terrestre, aunque el uso relativo sugiere el orden de preferencia para águilas asi: montano > brezal > pastizales toscos > helechos > pastizales finos > pantanos > bosques de hoja ancha > bosque pre-matorral >Bosques post-matorral > pasturas > otros hábitats. Las elevaciones variaron desde el nivel del mar hasta 900 m pero pareció que las águilas prefieren elevaciones entre 150-549 m. Con base en los datos de estas águilas, construimos un modelo simple para definir los límites probables de los territorios y para identificar áreas dentro de aquellos límites que probablemente son importantes para las águilas. Las características del modelo incluían los centros de los rangos identificados a partir de la localización de los nidos, los datos del uso de los nidos, los limites con los vecinos mas cercanos a mitad del camino entre los respectivos centros de sus nidos, y un corte de 6 km en las direcciones donde los vecinos no fueron claramente conocidos. El modelo designó áreas núcleo de 2–3 km de radio usando información sobre la densidad local de anidación de la águilas. Afuera de las áreas núcleo, las bajas elevaciones

fueron evitadas. Nosotros discutimos las ventajas y deficiencias del modelo y su robustez cuando es extrapolado a otras partes de Escocia.

[Traducción de César Márquez y Victor Vanegas]

In the British Isles, the breeding range of Golden Eagles (*Aquila chrysaetos*) has been much reduced. Today, Golden Eagles are found primarily in the Highlands of Scotland, although a few pairs breed in southwestern Scotland and northern England (Watson and Dennis 1992, Gibbons et al. 1993, Green 1996). In recent years, numbers of breeding Golden Eagles in Britain have been stable at about 425 pairs, although regional fluctuations have occurred (Dennis et al. 1984, Green 1996).

Afforestation of parts of upland Scotland has had a large effect on the habitat of the country. Preliminary studies have associated large-scale afforestation with the decline in the numbers of breeding eagles in western Scotland (Watson et al. 1987), and breeding success in western and southwestern Scotland (Marquiss et al. 1985, Watson 1992) has been shown to be dependent on afforestation. Watson et al. (1987) predicted that forestry would have a negative effect on eagles if it exceeded 40% of the area within 4 km of the center of an eagle's territory.

The Golden Eagle is an "amber list" species of medium conservation concern in the United Kingdom (Gibbons et al. 1996), because it has an unfavorable conservation status in Europe due to its rarity (Tucker and Heath 1994). The European population amounts to 5000–7200 pairs of which 5.8–8.4% are in the United Kingdom.

Between 1991-96, the Royal Society for the Protection of Birds (RSPB), working with the Research Division of the Forestry Commission, conducted a study of the ranging behavior of Golden Eagles in Argyll, Scotland. The primary aim of this study was to capture and fit backpack-mounted radiotransmitters to free-flying eagles and to follow their movements, and then to relate these data to both land cover and land use. As a product of this research, a simple model mapping eagle ranging behavior was constructed. The advantages of this mapping model are that it is easy to use, requires that the user has little a priori knowledge of eagles in general or of particular pairs, and is robust even when information on eagle pairs is limited. The mapping model was published as a Research Information Note by the Forestry Commission in the United Kingdom (McGrady et al. 1997). This paper presents the mapping model and discusses its advantages and shortcomings.

STUDY AREA AND METHODS

The study area covered about 500 km² in mid- and south Argyll, Scotland (Fig. 1). Both fresh and saltwater lochs are present, and the topography is hilly, with some peaks over 950 m. In general, the agricultural potential of the area is limited, with most land being capable of supporting only rough grazing and plantation forestry Some agricultural improvement has occurred such as drainage and fertilizing but this is generally limited to areas at lower altitudes.

Purple moor grass (*Molinia caerulia*) and white bent (*Nardus stricta*) dominate the areas grazed by sheep, and there are areas of poor condition dwarf-shrub heath. In some areas, bracken (*Pteridium aquilinum*) cover is extensive. Large and small blocks of commercial coniferous plantation (mostly *Picea sitchensis*) are quite common.

In terms of land use, sheep rearing and forest plantations are the predominant forms of land use. Some deer stalking is pursued but there is relatively little management of moors for Red Grouse (*Lagopus lagopus scoticus*) Watson et al. (1987) reported a general decline in grouse stocks in the area due to overgrazing.

Land cover, land use, terrain, and precipitation vary from region to region within the breeding range of Golden Eagles in Scotland. In general, the east mainland including the Cairngorms is drier, with higher elevation, and supports relatively more grouse moor and relatively less sheep rearing than in the west mainland. The islands of the Hebrides are also variable. Their climate is oceanic and few grouse are present.

Eagles were trapped in funnel traps and using a power snare (McGrady and Grant 1996). Transmitters were fitted as backpacks with a degradable link. They weighed 45 g and had a potential life of up to 4 yr. There was no evidence that the tagging of eagles, even both members of a pair, affected breeding or any other activities, and some eagles fitted with tags have bred in years after being instrumented.

Normally, tracking was done by at least two people in radio communication with one another. Immediately after fitting an eagle with a transmitter, it was followed intensively to make sure that it was able to fly properly After some days, birds newly fitted with transmitters were worked into the rotation of radio monitoring; thereafter they were visited as often as possible on a regular basis Because of logistical constraints, it was unusual to track eagles in more than one territory per day.

Birds were tracked using a directional (yagi) antenna and a compass to generate a bearing of the eagle's direction. From this, we could triangulate and estimate the location of the eagle. Our minimum aim was to get one high quality location (<100 m accuracy) per day of tracking. We often exceeded this aim. Because the most accurate locations were not from triangulation but from



Figure 1. Study area in western Scotland.

direct observations, we aimed to visually locate eagles. Once in view, we would observe eagles throughout the day, mapping their movements. Our observation locations were chosen so that we were able to record ranging of the eagles without influencing their movements. When eagles moved from our view, we would search for them, establish new observation points, and map their locations. Often, we had more than one eagle in view because all instrumented birds were paired.

In the analyses, we used only locations known to be <100 m accurate. Data were sorted to promote independence between fixes. Analysis suggested that fixes from any one individual eagle should be separated by >20 min

to ensure independence; we separated successive locations by at least 1 hr.

We used MacAulay Land Use Research Institute (MLU-RI) Land Cover Scotland 1988 (LCS88) (MacAulay Land Use Research Institute 1989) data augmented by maps from Forestry Commission and private forestry companies to map land cover. Fifty-six LCS88 land cover types were found within Golden Eagle ranges. These types were aggregated by shared primary land cover feature into 16 land cover types: wetlands, coarse grassland, smooth grassland with scrub, smooth grassland without scrub, water, anthropogenic, salt marsh, cliff, bracken, grass, heather, montane, improved pasture, pre-thicket forest/low scrub, post-thicket forest, and broadleaf forest. Details of the terrain were recorded on a digital terrain map using a Geographic Information System (GIS).

Preference for land cover types or elevation was analyzed using Generalized Linear Modeling (GLIM) procedures, and the approach used was that used by Heisey (1985). GLIM output yields estimates of the standard errors of individual values of habitat use, and the statistical significance of the variation in relative density among land cover or elevation can be estimated by a randomization test (Manly 1991). A score was calculated, which described the variation among the relative density values for each habitat. Using the higher of either the expected or observed number of locations as a weighting, the labels of the habitats found in each home range were shuffled. The log-linear model was then fitted to the randomized data and the variation score was compared with that from the real data. Randomization was performed 1000 times and the number of times the score was greater than the real score was used to obtain P values. Because response variables were counts, we tested errors against a Poisson distribution and used a log link (Crawley 1993).

In creating the model to map eagle ranges, we looked for features of ranging that were common to all birds. We attempted to make the model easy to use requiring little *a priori* knowledge of eagles or the area in which the model was applied.

RESULTS

We fitted 11 eagles with radiotransmitters. A total of 8 territory-holding adult eagles was radiotracked in all seasons from 1991–96. Because of radio failure, only seven adults provided enough data to analyze ranging behavior. We estimated the Minimum Convex Polygon (MCP) home range to be 7384 ha (range = $3967-12\,835$ ha). Core areas based on 50% of locations averaged 481 ± 192.3 (\pm SD) ha.

Based on consistent habitat use patterns among eagles, we developed a model for eagle ranging behavior based on the following features:

Range Centroid. The center of ranging was described by the harmonic mean center of ranging points. For any individual, this location was influenced by factors including terrain, distribution of prey, dominant wind conditions, season, year, nearneighbor distance, and breeding status. The ranging center could be estimated by using the location of the nesting site and the mean of all nesting sites was a good surrogate for the center of ranging (mean distance between mean of nest sites and harmonic mean of ranging locations = 26.8 ± 22.6 m, N = 7). By weighting the mean in accordance with recent use of particular nests, this estimate was improved (mean distance between weighted mean of nest sites and harmonic mean of ranging locations = 10.65 ± 7.45 m, N = 7). Even when terrain

clustered nests, the mean of each cluster gave good estimates of range centroids with multiple centers of activity. By identifying clusters of nests in one range and calculating two centroids from nest locations, the difference between harmonic mean locations and centroids for all eagles averaged <10 m.

Range Boundaries. Eagles could potentially range very far. However, in our study, they stayed within a 9 km radius of the centroid (Fig. 2). In most ranges, eagles were constrained by near neighbor, terrain features, or inappropriate habitat so they did not range equally in all directions. Ninety-eight percent of all locations were within 6 km of range centers.

Eagles are territorial and generally try to exclude intruding eagles, especially during prebreeding and breeding. When centroids of nearest neighbors were <12 km, the boundary between territories was a line equidistant from the two centroids.

Core Area and Centricity. All radiotracked eagles had core areas or places where >50% of locations occurred. In our study, core areas were all within 3 km of centroids. In general, core areas were smaller in areas where breeding density was highest. When plotted, the relationship between core area and local eagle density was inverse, and almost a straight line. We had too few data to test the significance of this relationship because we did not include ranges that were coastal or did not have neighbors in all directions.

An extension of the core area feature was that eagles used areas that were farther from the center of the range less than we expected. Figure 2 shows the distribution of eagle locations 0.5–6 km from the harmonic mean center, in relation to the amount of land available (open water areas excluded). Therefore, all other things being equal, if two areas of similar habitat were considered, the one closest to the range center would be the one most used by eagles.

Elevation Cut Off. Eagles showed significant selection of elevations between 150–550 m in western Scotland (Fig. 3).

Terrain. Eagles appeared to use certain terrain features more than others. Terrain features such as slope and aspect, along with wind direction and speed, determined places where updrafts were produced, and where soaring conditions are most favorable.

Landcover. Analysis of land cover choice by ea-



Distance from Territory Center (meters)

Figure 2. Relative density of Golden Eagle ranging locations in relation to available land area at different distances from the range center (harmonic mean). Number of territories = 6, number of eagles = 9, number of observations = 815).

gles showed there to be no significant selection of land cover types by eagles (Fig. 4). We ranked the most preferred to least preferred land cover types as follows: montane > heather > coarse grassland > bracken > smooth grassland with scrub > bog > broadleaved forest > pre-thicket forest/low scrub > post-thicket forest > improved pasture > water > anthropogenic > smooth grassland without scrub > salt marsh > wetlands > cliff. By further aggregating similar habitats, the rank of most



Figure 3. Relative use of elevation bands (from GLIM) within ranges by Golden Eagles in western Scotland. Number of territories = 6, number of eagles = 9, number of observations = 815).

preferred to least preferred landcover was: montane > grass > heather > high forest > bog > pre-thicket forest > other woodland > water. The main feature to note was that habitats most used by Golden Eagles were open ones, and the less used habitats were those that were either closed (i.e., had trees), those where human disturbance was likely, or those that had no hunting potential (i.e., water). Low use of cliff areas might have been a product of cliffs being difficult to interpret and map from the aerial photographs used to create LCS88.

Using the Model. The model requires some knowledge of the location of nesting places of eagles. From this, the model allows one to draw likely boundaries and estimate core areas of Golden Eagles in Scotland (Table 1). Our analysis also provides guidance to interpreting which areas within the model boundaries are most likely to be favored by eagles.

DISCUSSION

To date, our model has proven to be a useful starting point in discussions between developers, conservation agencies, and land-use regulators. For all parties, it has been useful in identifying areas in which conservation concerns are greatest for Golden Eagles, and has therefore concentrated discussions on areas whose loss would most likely impact eagles. It has provided the basis for the de-



Figure 4. Preferences for land cover types shown by radiotagged Golden Eagles in western Scotland. Y-axis is the relative preference (from GLIM) for each habitat type.

velopment of new models that take into account elevation, distance from centroid, and terrain to better predict use of areas by eagles, especially those that are outside the core (Whitfield et al. 2001).

When compared to maps drawn by local eagle experts from other parts of Scotland, the model predicts core area and range boundaries very accurately (McGrady unpubl. data). Predictions of the use of various elevations by eagles appear to be most accurate in areas with topography similar to our study area. Although the model can give good estimates of range boundaries and core areas, interpreting the variance between the model and actual eagle ranging is best done with some knowledge of eagles in general and local knowledge of individual eagles. This is true also for interpreting our analyses where features of eagle ranging are not so clear-cut, such as habitat selection. Boundaries were not solid barriers and specific terrain could shift them somewhat with the direction of the shift influenced by wind direction and velocity that might change which neighboring pairs have the most advantageous soaring conditions. Territoriality is not 100% efficient, so unchallenged intrusions did occur, but in general the intrusions between neighbors were never deep into adjacent ranges.

Based on direct observational data from other areas in Scotland where elevation is different than in our study area, it appeared that this elevation preference may be scaled according to the overall elevation of the range. In areas where ranges are at relatively high elevation (e.g., Cairngorms), the cutoff appeared to occur at about 150 m above the valley floor. In lower-lying areas (e.g., coastal sites on Hebridean islands), there appeared to be no elevation cutoff and eagles used all elevations.

In general, our examination of the use of land cover was related to its importance as habitat for potential prey for eagles. In other countries, where updrafts produced by solar radiation are important, certain types of land cover (e.g., scree) are favored (Brendel pers. comm.).

Although our model has proven to be a good guide to eagle range use, in places where there is local expertise on particular pairs, the model should be used within the context of that expertise. Although the model has been robust enough to prove a good predictor of eagle range boundaries in other parts of Scotland, there are some ranges where it does not perform well. These ranges do not have neighbors on all sides and have prey that is concentrated in areas away from the core area. These situations can result in eagles ranging farther than predicted and being found more often than expected outside of the model's core area.

There are instances where we believe the model has been inappropriately applied when not used in the context of local knowledge of eagle ranges. The extent of this problem is unknown. It is true that local knowledge of eagles may be somewhat biased because of the way in which the data were collected. Despite this, data gathered by local exTable 1. Steps involved in the use of the Golden Eagle ranging model.

STEP 1. FINDING THE RANGE CENTER	The range center is best calculated from the mean position of nests used in the past 10 yr, but lacking these data use the mean position of all nests. If the same nest is used on three occasions, enter its location three times into the calculation of the mean. In some territories, geo- graphical features cause nests to fall into separate clusters. In these, the mean position of each nest cluster should be calculated, and if their centers are ≥ 2 km apart, then the range will contain more than one center.
STEP 2. DETERMINING THE CORE AREA	The core area (where eagles spend 50% of their time) can be estimated by a circle around the range center with a radius of 2–3 km. The dis- tance that best estimates the core area is a reflection of territory quali- ty, prey distribution, and geographical features. In general, one would expect territories with abundant prey to have smaller core areas, and those with much unsuitable habitat (including plantation forest) or low prey densities to have larger core areas.
STEP 3. DETERMINING THE TERRITORY BOUNDARY WITH NEAR-NEIGHBORING EAGLES	To estimate the territory boundaries between two neighboring pairs of eagles whose nest centers are <12 km apart: (1) draw a straight line joining the two range centers, (2) find a point on this line halfway be- tween centers, (3) draw a line through the halfway point at right an- gles to the first line. To estimate the boundary with other neighbors repeat these steps until the line drawn forms a polygon around the range center. The strength with which this boundary is defended de- creases as one moves away from range center, and varies with season. The exact position of this boundary may vary with topographical fea- tures and windflow that produce favorable flying conditions.
STEP 4. DETERMINING THE TERRITORY BOUNDARY WHERE THERE ARE NO NEAR-NEIGHBORING EAGLES	Most eagle territories extend 6 km from the range center. Some eagles will use areas up to 9 km from their range center in the absence of neighbors or geographical boundaries. To determine the boundary, draw a curved line at 6 km radius from the range center to connect adjacent boundary lines drawn in Step 3. Eagles travelling farther are usually making use of a reliable source of food, such as a rabbit warren or a carcass, in areas not occupied by neighboring eagles.
STEP 5. USING AN ALTITUDE CUTOFF	In Scotland, eagle territories can be grouped as high altitude (e.g., Cairn- gorms), medium altitude (e.g., mainland Argyll), or low altitude (e.g., Isle of Mull). Eagles in medium and high altitude territories avoid low ground. For medium altitude territories, use an altitude cutoff at 150 m outside the core area, but include all altitudes within the core area. Use this rule in conjunction with steps 3 and 4 to delineate the outer edge of the eagle territory. High altitude territories exhibit an altitude cutoff outside the core area of 150–200 m above the valley floor. In low-lying coastal territories, eagles can use all altitudes except areas with a high level of human activity. Particularly in high and low altitude territories, local information is crucial to decide that altitude cutoff to use.

perts often provide critical information by which the results of the model should be interpreted. In some cases, data gathered by local experts can be analyzed carefully to lessen the influence of biases.

The basis of the model is the location of nests. This information is often closely held by eagle workers, conservation groups, and government agencies. There is a suspicion in the minds of some that the model should not be used by anyone other than those normally privy to this information. Of course, developers, foresters, landowners, and farmers are reluctant to accept judgments on land use change applications that are not totally transparent and open to discussion and negotiation.

Although we have not undertaken an exhaustive or systematic study of whether this model works elsewhere, where we have applied it in other places in the world, it has performed surprisingly well. It may be that some of the basic features of this model are the result of Golden Eagle energy budgets and the cost of efficiently maintaining a pair bond and territory.

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