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Brief report

Mirrored sequences of colonisation and abandonment by pairs of Golden Eagles *Aquila chrysaetos*

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We report colonisation by extra breeding pairs of Golden Eagles, and subsequent abandonments, in part of northeast Scotland during 1895–1985. The number of pairs rose from three in 1895–1937 to eight by 1948, and then fell to four during 1959–71 in reverse of the colonisation sequence. This fits the concept of hierarchic quality of habitat used, or of bird quality. Possible mechanisms to explain this are discussed.

1. Introduction

Most studies on density of Golden Eagles in Scotland have been short, emphasising differences amongst areas (Brown & Watson 1964, Newton 1979, Watson *et al.* 1992). During a 37-year study in 1944–80, Watson *et al.* (1989) recorded changes in the number of pairs within a single area in upper Deeside, Scotland. An increase of breeding pairs in the 1940s was associated with a rise of food potential in the form of more prey animals and more carrion from Red Deer (*Cervus elaphus*). Then a decline in 1959–71 followed a large reduction of deer carrion, associated with a higher proportion of the deer population being shot.

Below, we record a sequence of colonisation and then abandonment, a sequence which Watson *et al.* (1989) had not realised. The null hypothesis is that the sequence of colonisation makes no difference to the sequence of abandonment, and hence that the latter is random relative to the former. The alternative hypothesis is for the latter to be non-random relative to the former. Here we test these hypotheses.

2. Methods

We used a 400-km^2 area in northeast Scotland which included the 360 km^2 "core area" of Watson *et al.* (1989). The landowners' interests were mainly the shooting of Red Deer, with less interest in shooting Red Grouse (*Lagopus lagopus scoticus*). The area lies within that of the since formed Cairngorms National Park, designated in 2005.

Most of the area is moorland with much Heather (*Calluna vulgaris*). Forest in prehistoric times, the area was largely deforested by prehis-

toric farmers, and has since been kept as moorland by burning, prehistoric cultivation and domestic animals eating young trees. Since about 1800 the moorland has been maintained by deer eating tree seedlings. The bottoms of the glens (narrow valleys) have some grassland. Several glens carry stands of old Scots Pine (*Pinus sylvestris*) and Downy Birch (*Betula pubescens*), conifer plantations and fenced enclosures for natural reforestation. Alpine land rises above 760 m. More detailed descriptions of the area have been published along with an account of the eagles' food supply (Watson 1957, Brown & Watson 1964, Watson *et al.* 1989, 1992).

Commonly in animal behaviour, a home-range is where an individual animal lives, and a territory is a smaller part where an individual dominates all others of the same sex. Golden Eagles in each home-range typically use different nests in consecutive years, on our area (Watson 1957, Watson *et al.* 1989) and generally (Watson 1997). The nests usually occur in a cluster within the central part of the home-range, one nest being used in each cluster each year. The distance between nearest-neighbour nests in different clusters significantly exceeds that within clusters, for instance in our area (Watson & Rothery 1986). Adults in a pair display aggressively to other pairs, which led Watson (1997) to use the word "territory". However, whether they occupy territories with the above definition is unclear, so we use "home-range", and take the occupancy of each cluster as equivalent to the occupancy of a home-range. Our criterion for deciding whether two pairs occupied two adjacent clusters rather than one pair taking over both of them is that a nest in each cluster must hold eggs or young at the same time. A conservative criterion, it is the only one that is reliable in the absence of marked birds.

Information on nest occupancy in and before 1942, and some information in 1943 and 1944, came from talks with informants by one of us, Adam Watson (AW) in 1944–84. His first talks included Seton Gordon, who recorded nesting in Deeside during the early 1900s and occasionally afterwards. Subsequently, AW discussed nesting with many deerstalkers who had lifetimes of experience of the area, and who passed on information from their father predecessors (Acknowledgements).

All informants told AW that no estate staff persecuted eagles back to at least 1880. In 1943–2008, our own observations and local informants concur that this has applied since, with one exception. Within one nest-cluster in the late 1970s, a deer stalker burned heather on two crags with nests and no young fledged in several years, but an adult pair was present and laid eggs in most years.

AW made his first observations in 1943 and on comparing the above records with his own fieldwork, concluded that the informants knew all nest-clusters. He surveyed nest occupation by all pairs in the study area annually in and after 1945, using methods described in detail elsewhere (Watson 1957, Brown & Watson 1964, Watson *et al.* 1989). A.G. Payne and Stuart Rae made observations in the 1970s and 1980s.

3. Results

Birds continually used the same nest sites, including some crags and trees that have held nests since the 1890s. The number of breeding pairs of Golden Eagles rose from three in 1895–1937 to eight by 1948, and then fell to four during 1959–71 in reverse of the colonisation sequence (Table 1). In 1895–1937 there were three pairs. A fourth pair began nesting in 1938, a fifth in 1940, and a sixth in 1942. The seventh pair settled in 1947 and the eighth in 1948. All new nest-clusters lay between home-ranges that had been occupied long-term.

In 1959–66, numbers fell from eight pairs to five. Cluster 8, the last to be colonised, was first to be abandoned, after a last nesting in 1959. During 1962 the pair in cluster 7 nested there for the last time. Then in 1963–65 the adjacent pair that had nested in cluster 5 used nests in the vacated cluster 7 as well as in 5, but neither cluster held a separate pair in 1966–71. Since then, only ranges 1–4 have held breeding pairs. Birds there have used nests that were formerly in clusters 5 and 6, and two new nests that formerly did not occur, as well as frequent use of established old nests in clusters 1–4.

In statistical terms, colonisation took the sequence 4, 5, 6, 7 and 8, and abandonment the reverse sequence 8, 7, 6 and 5. The probability that this order of abandonment of four ranges was random is a permutation sum, given by 1 in 4! (i.e., 4 factorial or $4 \times 3 \times 2 \times 2$; $P = 0.042$). Likewise, the

Table 1. Sequence in which Golden Eagles occupied new nest-clusters and later abandoned them. Birds occupied nest-clusters 1–3 throughout. Note: Watson *et al.* (1989; figure 1c and p. 341) stated that a fourth pair occurred for five years in the 1970s, but observers found no eggs, young, or nest-building and did not distinguish individuals by plumage, so we now reject this record.

Nest-cluster	1895–1937	1938–1939	1940–1941	1942–1946	1947	1948–1959	1960–1962	1963–1964	1965–1966	1967–1985
8						+				
7					+	+	+			
6				+	+	+	+	+		
5			+	+	+	+	+	+	+	
4		+	+	+	+	+	+	+	+	+
3	+	+	+	+	+	+	+	+	+	+
2	+	+	+	+	+	+	+	+	+	+
1	+	+	+	+	+	+	+	+	+	+

probability of range 4 continuing as it has done and not being abandoned earlier than the others is 1 in 5! (P = 0.008). These results refute the null hypothesis that the sequence of abandonment was random relative to the sequence of colonisation. They confirm the alternative hypothesis that it was non-random, and indeed it mirrored the colonisation.

4. Discussion

The sequences of colonisation and abandonment of home-ranges by Golden Eagles and the associated use of their nest-clusters mirrored one another. A possible reason is that ranges were occupied and abandoned in order of quality, the first to be colonised being best, and the last to be colonised (and the first to be abandoned) poorest.

Food and nest-sites are fundamental requirements for breeding birds (Lack 1954, Newton 1998) and likely to be important features determining an area's suitability for breeding eagles. In this study we can rule out the availability of nest-sites as a limiting factor, because unused nest-clusters occurred in years when fewer birds bred. Nevertheless, differences in nest-site quality may have been involved.

Most studies on nesting density of Golden Eagle have made comparisons amongst study areas over a short run of years (e.g., Watson *et al.* 1992). In a long-term study of density in a region that included our area, Watson *et al.* (1989) found that the number of breeding pairs changed over the years in association with changes in food abundance. However, they did not know the individual hunting ranges and did not measure differences in food amongst different parts of their study area. In the present study of numbers in our area changing amongst years, numbers rose and then fell in reverse sequence. This fits the idea of a hierarchic value to different parts of the area, perhaps involving food availability, but one cannot rule out bird quality and other associated factors that have not been measured.

We do not know the origins of birds involved in the colonisation, or what happened to any missing birds. There might have been an increase in the number of Golden Eagles in the much wider Highland region during the period of increase, resulting in more birds occupying our area and other areas, and a subsequent decline in regional numbers during the period when fewer nest-clusters were used in our study.

These periods coincided with those of the Second World War and afterwards, during which there might have been less and then more killing of Golden Eagles in the wider Highland region while many gamekeepers were away in the armed services and then returned to their former local jobs. However, this is conjecture.

Nesting-territory occupancy has been used as a measure of territory quality in Black Kite (*Milvus nigrans*) where food availability was a factor (Sergio & Newton 2003). Furthermore, many owl (Strigidae) species which feed on voles (*Microtus* spp.) respond to food availability with short-term occupancy and abandonment of nesting territories, such as the Tengmalm's Owl (*Aegolius funereus*) which breeds in the areas of greatest food variety

in most years and in poor food-quality areas only in years of peak vole numbers (Korpimäki 1988).

The sequence of use of nest-clusters might also have been influenced by some other measure of quality, e.g., shelter from bad weather or differences in human disturbance. The occasional use of nests in abandoned nest-clusters, during years when adjacent more continuously used nest-clusters were not used, would fit this and also any hierarchic quality in nest sites.

We suggest that the mirrored sequences of colonisation and abandonment of home-ranges by Golden Eagles are a consequence of some aspect of hierarchic quality. It would be useful if the mirrored sequences, as well as possible mechanisms to explain them, could be tested by new observations elsewhere. Future work on individually marked birds, within individual home-ranges, on food supply and habitat, in relation to the constancy of range occupation might help understand how Golden Eagles space themselves within habitats of varying quality.

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Raportoimme maakotkan (*Aquila chrysaetos*) pesimäpaikan asuttamiset ja niitä seuraavat hylkäämiset Koillis-Skotlannissa 1895–1985. Parimäärä nousi jakson 1895–1938 kolmesta vuoden 1948 seitsemään ja laski neljään jaksolla 1959–1971 käänteisesti asuttamisjärjestykseen nähden. Havainnot tukevat teoriaa elinympäristön hierarkkisesta laadusta.

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