

The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland

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Abstract

Several studies have documented negative effects of persecution by humans on the population dynamics of large birds of prey. Several areas have seen a reduction in persecution in modern times, but the demography of large raptors still makes these birds vulnerable to such effects. In a GIS analysis, utilising data collected during two national censuses of the golden eagle *Aquila chrysaetos* in Scotland and contemporary data on the distribution of poisoning incidents (a common method of raptor persecution in Scotland), we show that persecution was associated with a reduction in the age of first breeding, territory vacancies, and the use of territories by non-breeding immatures. Persecution was therefore reducing adult survival and distribution and was probably creating ecological traps that attract mobile immatures, increasing subadult mortality in birds that may originate from persecution-free areas. Mapping a form of land management unique to moors managed for red grouse *Lagopus lagopus scoticus* shooting, where most poisoning occurs, we also show similar associations between golden eagle demography and grouse moor management. As such, persecution may be having a major impact on the golden eagle population of Scotland, since it occurs over a wide area and at least in some areas has continued unchecked over many decades.

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1. Introduction

Birds of prey are some of the most threatened birds in Europe (Tucker and Heath, 1994) and many are classed as vulnerable on Annex I of the EC Wild Birds Directive. Understanding the causes of the perilous conservation status of such species has generated considerable research effort and results point to many contributory influences, including habitat loss and, especially for larger species, electrocution at power poles and persecution by humans (e.g., Ferrer and Hiraldo, 1991; Real and Mañosa, 1997; Pedrini and Sergio, 2001, 2002). Persecution of raptors can take many forms, including destruction of nests, deliberate disturbance of nesting birds, and poisoning, shooting and trapping of adults

and immatures (e.g., Watson, 1997). Consequently, it can have several demographic costs for raptor populations. In parts of Scotland, for example, persecution has reduced breeding productivity of golden eagles *Aquila chrysaetos* by 20% (Scottish Raptor Study Groups, 1997). But it is the killing of adults and immature (subadult) birds that is potentially a more severe problem, owing to the life history characteristics of eagles (e.g., Real and Mañosa, 1997).

Several studies have shown a spatial coincidence between low adult survival and high levels of persecution (e.g., Etheridge et al., 1997; Real and Mañosa, 1997; Real et al., 2001). Because persecution is frequently associated with game hunting activities (Etheridge et al., 1997; Villafuerte et al., 1997; Real et al., 2001; Whitfield et al., 2003), it is most likely to limit raptor numbers and distribution in areas where game is hunted (Moore, 1957; Newton, 1979; Gibbons et al., 1994; Etheridge et al., 1997; Villafuerte et al., 1997).

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Furthermore, the effect of persecution can spread through a population over even larger areas, beyond the boundaries of where persecution actually occurs (Newton, 1998; González et al., 1989). This can happen if a population is migratory or if persecution-areas are attractive to birds establishing territories. In such cases, persecution-areas may act as 'sinks' for the population, drawing in birds from persecution-free areas (Newton, 1979). In addition, in many large raptors, juveniles can disperse over considerable distances away from natal territories to congregate in food rich areas without breeding adults. As they become closer to breeding age, they increasingly return to the natal area to seek out a breeding territory (Haller, 1982; Steenhof et al., 1984; Ferrer, 1993; Real and Mañosa, 1997; Alcántara et al., 2001). So, if young birds from persecution-free areas disperse into other areas where they are killed by humans, this can reduce breeding numbers in the natal area by raising subadult mortality (Real and Mañosa, 1997).

Golden eagles typically start breeding as adults when they are 4 years old (Steenhof et al., 1983) and similar delayed breeding occurs in other large eagles and other large raptors (e.g., Gargett, 1990). Persecution of adult raptors can lower their numbers, creating territorial vacancies, so that nesting by subadults can occur (Newton, 1979). Although nesting by subadult raptors also occurs with an increased abundance of prey or in expanding populations (Newton, 1979, 1986; Village, 1990), in territorial eagles the trait has almost invariably been associated with increased adult mortality, with human interference as the most likely causal mechanism (Sandeman, 1957; Valverde, 1960; Novelletto and Petretti, 1980; Steenhof et al., 1983; Sánchez-Zapata et al., 2000; Balbontín et al., 2003). Populations of large raptors such as eagles, which are in a favourable status, usually contain a high number of non-breeding adult 'floaters' (Hunt, 1998; Kenward et al., 2000). These adult floaters replace adult breeders when vacancies arise in breeding territories, so increasing replacement of adult breeders by subadults is a strong indication that a population lacks the security afforded by a floating adult sector and so is at risk of decline (Newton, 1979; Hunt et al., 1998). Hence, Balbontín et al. (2003) have suggested that age at first breeding could be used as a warning of potential population decline (see also Kenward et al., 2000) and that conservation action (usually against human interference) should be targeted at those territories where subadult nesting occurs. Such action is warranted because, if persecution persists, territory vacancies can be created that result in gaps in distribution in the areas where persecution occurs and possibly also in other areas, depending on the severity of persecution.

Censuses of golden eagles in Scotland indicated that between 1982 and 1992 the number of birds occupying territories was stable at around 420 pairs (Dennis et al.,

1984; Green, 1996). Population stability belied the occurrence of many gaps in distribution, that have repeatedly been attributed to the effects of persecution, notably in the central and eastern Highlands, and in upland areas south of the Highlands, where moorland management for red grouse *Lagopus lagopus scoticus* shooting occurs (e.g., Green, 1996; Watson, 1997). Studies have also highlighted detrimental effects on eagle breeding success and age of first breeding in grouse moor areas (Sandeman, 1957; Watson et al., 1989; Scottish Raptor Study Groups, 1997). Illegal use of poisons in the uplands of Scotland, a frequent method for killing raptors to which golden eagles as carrion feeders are especially vulnerable, is most frequently associated with areas where grouse moor management occurs (Whitfield et al., 2003).

Despite many studies suggesting a role for persecution in affecting the biology of golden eagles in Scotland, no study has examined rigorously any associations between territory vacancy and the occurrence of persecution or looked at whether persecution is associated with differences in age structure within the national population of golden eagles. In this paper, we use data gathered during two national censuses of the golden eagle in Scotland, and contemporary measures of persecution, to address three main questions: (1) is territory occupation by subadults and breeding by subadults associated with areas of persecution? (2) Do subadult pairs have poorer breeding success than adult pairs? (3) Are vacant territories more likely in areas of persecution?

2. Methods

We used the results of the two national censuses of golden eagles in Scotland, in 1982 (Dennis et al., 1984) and in 1992 (Green, 1996). These censuses attempted to visit at least twice in the same season every known golden eagle territory in Scotland. A first visit to a territory involved checking if it was occupied by a pair prior to egg laying (i.e., direct observation of a pair, or of a built up nest), with a second visit during the incubation phase to check for any evidence of birds having laid eggs or, if a territory was not found to be occupied on the first visit, to provide a second check for territory occupation. For occupied territories a third visit was made later in the breeding season to record the number of any young that had fledged or had reached an age where fledging could safely be assumed (Steenhof, 1987; Steenhof and Kochert, 1982). Several territories were kept under surveillance by observers in the years intervening the two national censuses and so data on breeding success (number of young fledged per year) were available for up to nine additional years.

Attempts were made to age all birds as either adult or immature (subadult) depending on plumage character-

istics, with adults (birds at least four years old) having no white in their plumage and immatures (birds less than 4 years old) having some white in the wing feather at the carpal joint and/or in the anterior portion of the tail (Hunt et al., 1995; Bloom and Clark, 2001). It was not possible to age all birds, however. We classed each territory as occupied either by a two adult pair (adult pair), an adult and an immature pair (mixed age pair), a two immature pair (immature pair), a single or group of immatures, or not used by any eagles (no eagles seen).

For each known territory recognised as a contemporary or former breeding territory, we calculated a territory centre that was the mean location of all used alternative nest sites (those used during a maximum period of 11 years, 1982–1992) or, if information on nest site use was not available, the mean location of all alternative nest sites (McGrady et al., 1997, 2002; McLeod et al., 2002a,b). Territory centres were entered into a Geographical Information System (GIS) (ArcView[®]) and taken as the location of territories. When looking for associations between particular features and different types of territories we used three distances, based on telemetry data collected in western Scotland (McGrady et al., 1997): within 3, 6 or 12 km. McGrady et al. (1997) found that most ranging was within 6 km of the territory centre, the ‘core’ of the territory (50% of activity) was within 3 km, and maximum range distance was around 12 km. Some former breeding territories may not have been used for several years and records of occupancy may have come from different years. So we cross-checked territory names or codes and assumed territories in different years with the same name or code were the same territory, verified by matching location coordinates in the GIS. We avoided the possibility that some of these ‘territories’ may have just been alternative nesting areas by discounting those territories whose centres or active nest sites were within 1 km of another centre or active nest site, unless there was evidence of simultaneous use.

As a measure of the distribution of persecution, we used data on poisoning incidents in Scotland collated annually by the Royal Society for the Protection of Birds (e.g., RSPB, 1999, 2001) for the years 1981–2000 inclusive (Whitfield et al., 2003). Although it is difficult to quantify features of an illegal and therefore largely covert activity, poisoning is the most frequently detected form of raptor persecution in Scotland. A poisoning incident involved evidence of the use (or intention of use) of a chemical (typically an agricultural pesticide) as a poison in an attempt to kill a scavenging or predatory animal. Evidence involved the discovery of either a dead or sick animal of any species containing levels of poison sufficient to cause the death or illness, discovery of bait (e.g., a carcass) laced with poison, or a cache of a chemical that could be used as a poison. All poisoning incidents involved circumstances of discovery that could

not be interpreted as the consequence of approved use under the Regulations governing the relevant chemicals. As our analyses were primarily concerned with spatial associations, we removed all data with a minimum location resolution of 10 km (to leave only data with a maximum location resolution of 1 km). We also removed all data that involved illegally cached or stored supplies of poison, since storage location may not necessarily reflect location of intended use. To avoid pseudo-replication we ensured that there was no duplication of records at the same or similar location (within 1 km) and date (within 1 month). Thus, records that involved, for example, several animals dying from contact with the same poisoned bait were classed as a single incident. For such records we calculated a mean location. Geographical grid references for the poisoning incidents were entered as a layer into the GIS.

Whitfield et al. (2003) showed that records of poisoning incidents in the uplands of Scotland were most closely associated with the distribution of ‘strip muirburn’ habitat. Strip muirburn results from land managers periodically burning heather moorland to stimulate new growth in heather *Calluna vulgaris*, the main food plant of red grouse. This management aims to create ideal habitat for red grouse (Muirburn Working Party, 1977; Hudson, 1992) and is uniquely associated with areas where shooting of red grouse occurs. Some grouse managers illegally control birds of prey because they believe that their predation on red grouse or their mere presence during shooting reduces the bags of driven grouse (e.g., Watson, 1997; Thirgood et al., 2002). Driven shooting of red grouse is a sporting tradition unique to the UK. It involves numerous beaters walking across moorland in autumn to ‘drive’ (flush into flight) coveys of red grouse over a line of butts (small low-walled shelters), from which several hunters attempt to shoot the driven grouse as they fly over and past. We entered the distribution of strip muirburn habitat as an additional layer in the GIS using the summary classes of the Land Cover of Scotland 1988 (LCS88: MLURI, 1993), as a surrogate for the distribution of moorland actively managed for red grouse (see Whitfield et al. (2003) for further details).

As a means of examining regional differences in parameters we used the bio-geographical divisions of Scotland derived by Scottish Natural Heritage (SNH, 1998). The SNH zonal programme has identified 21 Natural Heritage Zones (NHZs) that reflect the variation in biological and landscape qualities across Scotland (Fig. 1). NHZ boundaries were created as an additional layer in the GIS.

Our main approach was to overlap layers within the GIS to assess any spatial associations between the different parameters, notably between different types of territories and records of poisoning incidents or strip muirburn. We measured the distance to a poisoning

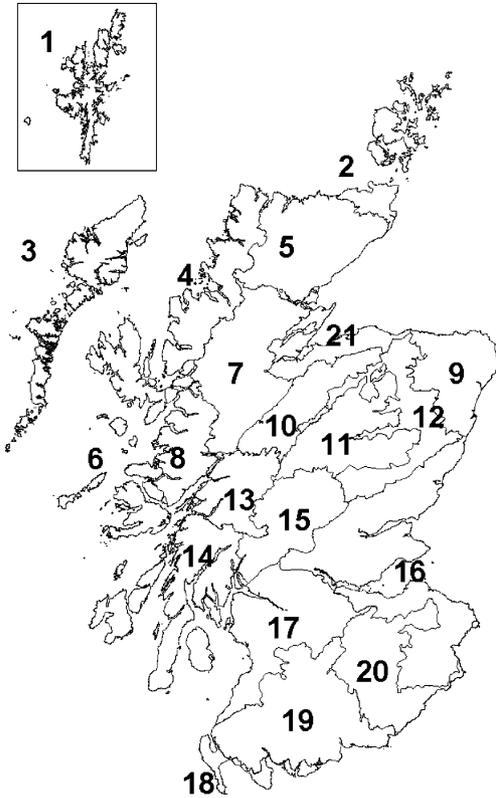


Fig. 1. Biogeographic zones of Scotland, termed Natural Heritage Zones (NHZs), developed by Scottish Natural Heritage (SNH, 1998). 1, Shetland; 2, North Caithness and Orkney; 3, Western Isles; 4, North West Seaboard; 5, The Peatlands of Caithness and Sutherland; 6, Western Seaboard; 7, Northern Highlands; 8, Western Highlands; 9, North East Coastal Plain; 10, Central Highlands; 11, Cairngorm Massif; 12, North East Glens; 13, Lochaber; 14, Argyll West and Islands; 15, Breadalbane and East Argyll; 16, Eastern Lowlands; 17, West Central Belt; 18, Wigtown Machairs and Outer Solway; 19, Western Southern Uplands and Inner Solway; 20, Border Hills; and 21, Moray Firth. For further details in the context of the golden eagle in Scotland, see Watson and Whitfield (2002).

incident or distance to strip muirburn from each known territory and cast these into appropriate distance bands for different territory types, specifically comparing such measures for territories occupied by adult pairs against measures for other types of territory in 2×2 contingency tables. Several territories could potentially be closest to the same poisoning incident, so that some poisoning incidents may have contributed undue weight in the analysis. Hence, we also took measures and conducted analyses from the contrasting perspective by calculating distances to the nearest type of territory from each record of a poisoning incident. We did not repeat these calculations for distances from strip muirburn, because a previous study had already established a strong spatial association between records of poisoning and strip muirburn (Whitfield et al., 2003). So our analyses involving this habitat were more by way of confirmation of the previous study.

We used stepwise logistic regression (with a logit link function) to see if the proportion of eagles that was adult in a geographical zone was associated with persecution intensity (indexed by the density of poisoning incidents). We also included breeding productivity (fledglings per occupied territory per year) for each zone in the 10 years preceding the year when the age structure was estimated (1992) as an additional potential explanatory variable since the production of young birds was an obvious alternative explanation of why zones may have differed in the proportion of birds that was adult. We used only those zones where there was productivity data for at least five territories ($N = 9$ zones). Ideally this analysis should only have considered productivity in the four years preceding 1992 (as these were the years which would have produced the subadults present in 1992), but this would have greatly reduced sample sizes. Productivity varies annually but covaries between regions (e.g., Watson et al., 2003), so relative differences between zones (the parameter of interest in the analysis) should have been similar regardless of the period considered. An interaction term was not included in the analysis because a preliminary analysis revealed it had no influence. The sampling of productivity was uneven between regions for the 10-year period (because not every territory was sampled for 10 years), so we also repeated the same analysis using 1982 productivity or 1992 productivity as an independent variable (i.e., years when sampling across regions was even because every territory was sampled, $N = 12$ zones). These years were not representative in respect of the absolute number of immatures across zones (because productivity varies annually) but may have better reflected differences between zones in productivity which, as argued above, was the parameter of interest and should have been immune to the actual period or year being considered. We also repeated the analyses using the proportion of birds that was adult in 1982 as the dependent variable.

As a result of previous studies (see Section 1), we expected that our surrogate measures of persecution (poisoning incidents) and grouse moor management (strip muirburn) would be associated with a reduced age of first breeding and territory vacancies. Our tests should therefore have been one-tailed, but as a conservative measure, we made our tests two-tailed. All χ^2 tests were corrected for continuity.

3. Results

3.1. Age and breeding success

Adult pairs were more likely to lay eggs than mixed age/immature pairs in both 1982 ($\chi^2 = 77.24$, $P < 0.001$) and in 1992 ($\chi^2 = 13.88$, $P < 0.001$), and were more likely to fledge at least one young in both 1982

Table 1
Age status of pairs of golden eagles in Scotland in the 1982 and 1992 national surveys and associated breeding success statistics

Year	Age of pair	Number of pairs					N young fledged
		Total	Breeding pair ^a	Non-breeding pair	Successful pair ^b	Unsuccessful pair	
1982	AA	333	238	95	160	173	183
	AS	33	0	33	0	33	0
	SS	11	1	10	1	10	2
1992	AA	331	206	125	109	222	123
	AS	38	17	21	3	35	3
	SS	15	1	14	1	14	1

A, adult and S, subadult.

^a A pair that laid eggs.

^b A pair that raised at least one chick to fledging.

($\chi^2 = 31.44$, $P < 0.001$) and in 1992 ($\chi^2 = 12.98$, $P < 0.001$) (Table 1).

3.2. Regional differences in subadult pairs and age structure

Overall, there were 89% adult pairs in 1982 and 85% adult pairs in 1992 but with marked regional differences in these proportions (range of values, for zones with at least five territories: 63–96% in 1982; 67–95% in 1992). Comparing the proportions of birds in pairs that were adult with the proportions of all birds seen that were adult, in relation to a measure of persecution intensity (density of poisoning incidents), revealed relatively more unpaired immatures in zones where poisoning was most intense (Fig. 2). This was most marked in 1992 when more unpaired immatures were seen. In other words, in zones where poisoning was more prevalent, unattached immature birds and subadult pairs formed larger proportions of the birds recorded.

In the logistic regression only the density of poisoning incidents was included in the final model (unstandardised coefficient = -0.128 ± 0.029 SE, $Z = -4.33$, $P < 0.001$) and breeding productivity was excluded ($Z = 0.38$, $P = 0.707$). The proportion of birds that was adult was negatively associated with the intensity of persecution (higher proportions of subadults were in zones with higher densities of poisoning) but was not associated with the fledging production rate. Hence, there were more subadults in zones with higher persecution, even though more subadults were not produced in these zones. All of the repeated analyses showed the same result, with only the density of poisoning incidents emerging as significant in the model ($P < 0.001$ in each case), with a negative influence on the proportion of birds that was adult.

3.3. Use of potential breeding territories by different age classes

If at least one subadult was seen in a territory but no adults were seen, the territory was classed as being used

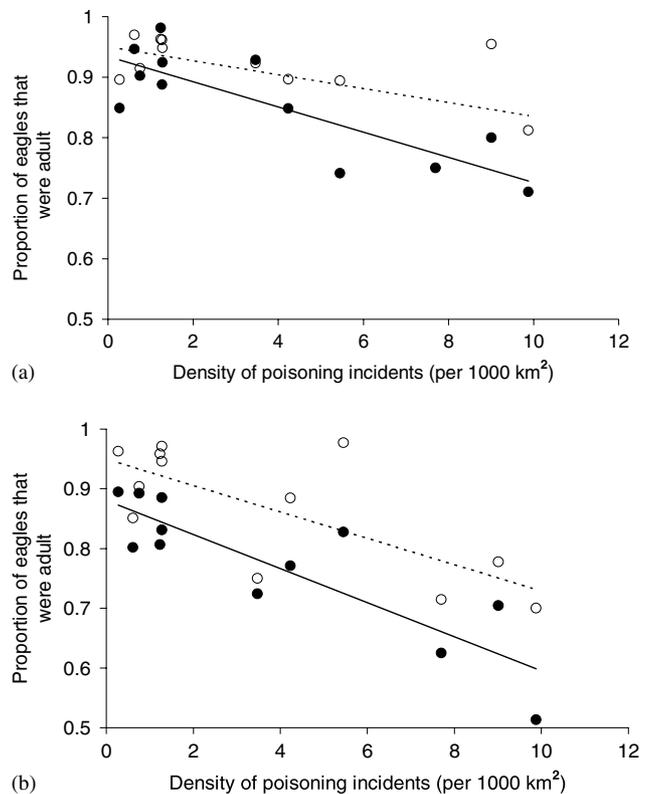


Fig. 2. The proportion of all territorial and non-territorial birds that was adult (filled circle) and the proportion of paired birds that was adult (open circle) plotted against the density of poisoning incidents in a geographical zone for (a) 1982 and (b) 1992. Linear trend lines are shown. Only zones with at least five occupied territories were included.

by subadults. For other territories we maintained the stricter definition of occupation by either adult or mixed age pairs.

In 1982 adult pairs were more likely to be associated with territories far away from records of poisoning incidents than were mixed age pairs or subadults (AA vs AS, Fisher's Exact Test $P = 0.004$; AA vs S, $\chi^2 = 8.31$, $P = 0.004$), but in 1992 only the contrast between territories used by adult pairs and subadults was significant (AA vs AS, Fisher's Exact Test $P = 0.31$; AA vs S, $\chi^2 = 33.17$, $P < 0.001$) (Table 2). Hence known territories

Table 2

Use of territories by adult pairs (AA), mixed age pairs (AS), subadults (S), and no eagles (none) according to their distance from a record of a poisoning incident

Year	Territory 'occupation'	Number of territories		Total
		<6 km from poisoning (%)	>6 km from poisoning (%)	
1982	AA	43 (12.8)	292 (87.2)	335
	AS	11 (33.3)	22 (66.7)	33
	S	13 (31.0)	29 (69.0)	42
	None	22 (26.5)	61 (73.5)	83
1992	AA	37 (11.0)	298 (89.0)	335
	AS	7 (16.7)	35 (83.3)	42
	S	19 (46.3)	22 (53.7)	41
	None	19 (16.7)	95 (83.3)	114

associated with incidents of persecution were more likely to be used by mixed age pairs in 1982 and subadults in both 1982 and 1992.

There was only a weak tendency for territories occupied by mixed age pairs to be more likely in areas of strip muirburn (grouse moors) than were territories occupied by adult pairs (1982: $\chi^2 = 1.99$, $P = 0.158$; 1992: $\chi^2 = 2.49$, $P = 0.115$), although territories used by subadults alone were strongly associated with areas of strip muirburn compared to those occupied by adult pairs (1982: $\chi^2 = 16.56$, $P < 0.001$; 1992: $\chi^2 = 11.4$, $P = 0.001$) (Table 3). For a more stringent analysis, we next examined the use of territories by different age classes in

the four zones (10, 11, 12, and 15) that had most poisoning incidents and most strip muirburn (and, hence, more grouse management) (Fielding et al., 2003; Whitfield et al., 2003). As strip muirburn was more prevalent in these zones than in others, we also decreased to 3 km the threshold distance a territory was considered to be associated with muirburn. Territories occupied by adult pairs were less likely to be associated with strip muirburn than territories that were occupied by mixed age pairs or subadults only in 1982, but not in 1992 when sample sizes were lower (Table 4).

The 394 poisoning incidents were closer than expected to territories used by subadults only and farther

Table 3

Use of territories by adult pairs (AA), mixed age pairs (AS), subadults (S), and no eagles (none) according to their distance from strip muirburn (i.e., high persecution) habitat

Year	Territory 'occupation'	Number of territories		Total
		<6 km from muirburn (%)	>6 km from muirburn (%)	
1982	AA	125 (37.3)	210 (62.7)	335
	AS	17 (51.5)	16 (48.5)	33
	S	30 (71.4)	12 (28.6)	42
	None	52 (62.7)	31 (37.3)	83
1992	AA	117 (34.9)	218 (65.1)	335
	AS	9 (21.4)	33 (78.6)	42
	S	26 (63.4)	15 (36.6)	41
	None	68 (59.6)	46 (40.4)	114

Table 4

Use of territories by adult pairs (AA), mixed age pairs (AS), and subadults (S) according to their distance from strip muirburn habitat within the high persecution zones 10, 11, 12, and 15 (see Fig. 1 for location of zones)

Year	Territory 'occupation'	Number of territories		Total
		<3 km from muirburn (%)	>3 km from muirburn (%)	
1982	AA	36 (66.7)	18 (33.3)	54
	AS	10 (100.0)	0 (0.0)	10
	S	19 (90.5)	2 (8.5)	21
1992	AA	33 (73.3)	12 (26.7)	45
	AS	3 (60.0)	2 (40.0)	5
	S	13 (86.7)	2 (13.3)	15

Fisher's Exact Tests: 1982, AA vs AI, $P = 0.05$; 1992, AA vs AI + I, $P = 0.757$; 1982, AA vs I, $P = 0.044$; 1992, AA vs I, $P = 0.483$.

Table 5

'Occupation' of known golden eagle territories by adult pairs (AA), mixed age pairs (AS), subadults (S) or no eagles (none), the status of territories nearest to a poisoning incident ("All poisoning incidents" – includes all incidents) and the status of territories nearest to those poisoning incidents that were within 12 km of a known eagle territory centre ("<12 km from eagle territory" – the maximum extent of ranging by a territorial eagle: McGrady et al., 1997)

Year	Occupation	All territories			All poisoning incidents			Poisoning incidents <12 km from eagle territory		
		%	LCL	UCL	%	LCL	UCL	%	LCL	UCL
1982	AA	49.7	45.9	53.5	<u>26.7</u>	22.3	31.0	<u>23.0</u>	17.1	28.9
	AS	4.9	3.3	6.5	8.9	6.1	11.7	12.8	8.1	17.4
	S	6.2	4.4	8.1	24.6	20.4	28.9	20.9	15.2	26.6
	None	12.3	9.8	14.8	21.6	17.5	25.6	23.5	17.5	29.4
1992	AA	49.7	45.9	53.5	<u>26.7</u>	22.3	31.0	<u>20.9</u>	17.3	26.6
	AS	6.2	4.4	8.1	3.6	1.7	5.4	7.1	3.5	10.7
	S	6.1	4.3	7.9	19.5	15.6	23.5	19.4	13.9	24.9
	None	16.9	14.1	19.7	31.7	27.1	36.3	27.6	21.3	33.8
Total		674			394			196		

LCL, lower 95% confidence limit; UCL, upper 95% confidence limit. Values are emboldened for those types of territories closest to poisoning incidents whose 95% confidence limits fell outside the 95% confidence limits for the overall percentage of the respective territory 'type' (in column "All territories"), illustrating that poisoning incidents were closer than expected to that type of territory. Values are italicised and underlined for those types of territories farthest from poisoning incidents (according to 95% confidence limits), illustrating that poisoning incidents were farther than expected from that type of territory. Percentage values that are given for each year do not sum to 100% because values for other types of territory (e.g., 'occupied' by single adults or unaged birds) are not presented.

than expected from territories occupied by adult pairs, in both 1982 and 1992 (Table 5). They were not closer than expected to territories occupied by mixed age pairs in either 1982 or 1992. Taking only those 196 poisoning incidents that were less than 12 km from a known golden eagle territory centre (i.e., within the maximum extent of breeding eagle ranging) gave similar results, except that poisoning incidents were also closer than expected to territories occupied by mixed age pairs in 1982 (Table 5).

3.4. Persecution and territories where no eagles were seen

Previously occupied territories where no eagles were seen were: (1) more likely to be associated with a record of a poisoning incident than were territories occupied by adult pairs in 1982 but not in 1992 (1982: $\chi^2 = 8.45$, $P = 0.004$; 1992: $\chi^2 = 1.97$, $P = 0.160$) (Table 2); (2) more likely to be closer to strip muirburn habitat than were territories occupied by adult pairs in both 1982 and 1992 (1982: $\chi^2 = 16.47$, $P < 0.001$; 1992: $\chi^2 = 20.45$, $P < 0.001$) (Table 3); and (3) were more likely to be associated with strip muirburn (in zones 10, 11, 12, and 15) than were territories occupied by adult pairs in 1982 but, probably due to a low sample size, not in 1992 (1982: $\chi^2 = 4.13$, $P = 0.042$; 1992: Fisher's Exact Test, $P = 0.259$) (Table 4).

Poisoning incidents were more likely to be closest to a territory in which no eagle was seen in 1982 or in 1992, regardless of whether all incidents or only those less

than 12 km from a known territory were considered (Table 5).

4. Discussion

In keeping with other studies of golden eagles (Steenhof et al., 1983; Sánchez-Zapata et al., 2000; Pedrini and Sergio, 2001), we found that subadult and mixed age pairs had lower breeding success than did adult pairs. We also found, however, that territories occupied by subadults were more likely to be in areas associated with persecution (see also Sandeman, 1957), so we cannot dismiss the possibility that lower breeding success was due to human interference (Scottish Raptor Study Groups, 1997) rather than some feature of the birds themselves (Newton, 1991; Espie et al., 2000) or differing food supplies. Steenhof et al. (1983) showed that territories occupied by subadult pairs did not appear to differ from territories occupied by adult pairs with respect to food but were more likely to suffer from human interference, and hence were of lower 'quality'. Ferrer and Bisson (2003) placed greater emphasis on the lower quality of territories occupied by subadult breeding Spanish imperial eagles *Aquila adalberti* rather than intrinsic differences between age classes as an explanation of why subadult pairs were less productive than adult pairs. Penteriani et al. (2003) showed that in a population of Bonelli's eagle *Hieraetus fasciatus* both territory quality and the age of breeding birds influenced breeding performance, with lower quality territories

used by subadult pairs having lower prey availability and greater human interference. We have no direct evidence that territories occupied by subadult pairs of golden eagles in Scotland contained less food than those occupied by adult pairs but it seems unlikely that they did, given that they were disproportionately found in areas of grouse moor which are usually rich in prey for eagles (e.g., Watson et al., 1989; Watson, 1997). Rather it seems most likely that low breeding success of subadult pairs in Scotland was the result of inexperience of occupying birds, human interference or a combination of both influences, as found by Steenhof et al. (1983) in Idaho, USA.

The association of subadult pairs with areas of persecution was most marked in 1982, perhaps because in 1992 there were more immatures present (Fig. 2), so it is possible that the occurrence of subadult breeding was in part related to the abundance of subadults. There was an indication, however, that persecution in the western Highlands of Scotland declined over the study period, becoming more restricted to areas managed as grouse moor in the eastern Highlands (Whitfield et al., 2003). Hence, our assumption in the present study of an unchanging distribution of persecution across the study period may have weakened any association between age of breeding and persecution in 1992 if by 1992 age of first breeding had increased in areas where persecution was reduced in the western Highlands.

Our study therefore provides support for the notion that in territorial eagles nesting by subadults is more common when numbers of adults are reduced through persecution by humans (Sandeman, 1957; Valverde, 1960; Novelletto and Petretti, 1980; Steenhof et al., 1983; Sánchez-Zapata et al., 2000; Pedrini and Sergio, 2001; Balbontín et al., 2003). The marked differences between areas in the proportion of adult breeding birds reflected differences in an index of the intensity of persecution. In areas with little evidence of persecution, in around 95% of pairs both partners were adult, but in areas where persecution was most intense, only in around 65–70% of pairs were both partners adult. Hunt et al. (1998) found that only 3% of territorial golden eagles were subadults in the Diablo Range of California where persecution was unknown, and also estimated a high number of non-breeding adult 'floaters'. By contrast, Sánchez-Zapata et al. (2000) showed that only 70–76% of golden eagle pairs in southeastern Spain were both adults and attributed this to a high adult mortality rate through human interference.

The clearest indication that an eagle population lacks the security of an adequate floating segment is a high incidence of subadults as members of breeding pairs (Newton, 1979). Hunt et al. (1995) also noted that the increasing occurrence of subadult breeders is indicative of a risk of a declining population. Building on these findings, and their own and others' studies of spatial

variation in demographic traits of Bonelli's eagle (e.g., Real and Mañosa, 1997), Balbontín et al. (2003) have suggested that age at first breeding should be used as an early warning of potential population decline and that conservation action against human interference should be targeted at those territories where subadult nesting occurs. The common finding in studies of European eagles, that territories which are not used by any birds are also more likely to be found in areas where human interference is greatest (e.g., Valverde, 1960; González et al., 1989; Haller, 1996; Real and Mañosa, 1997; Real et al., 2001; present study), serves to reinforce the notions that reduction in age of breeding due to human interference is a sign of an insecure population and that, consequently, conservation attention should focus on areas where interference is most prevalent. The strong implication of the present study is that persecution is directly restricting the distribution of golden eagles in Scotland, as previously suggested (e.g., Brown, 1976; Green, 1996; Watson, 1997).

Our results suggest that areas in Scotland where persecution was prevalent were not only associated with territories devoid of eagles and a reduction in the age of breeding eagles but also with use by non-breeding immatures. Dispersing young eagles are capable of long-distance movements in the search for prey rich areas where breeding eagles are absent, and several immature eagles may use these areas (e.g., Haller, 1982; Steenhof et al., 1984; Ferrer, 1993; Real and Mañosa, 1997; Alcántara et al., 2001): limited evidence from golden eagles in Scotland is consistent with this trait (Grant and McGrady, 1999). Watson (1997) showed that immature golden eagles in western Scotland (where persecution is usually low) may attempt to utilise the margins of occupied territories. But occupied territories are at high density in western Scotland (Dennis et al., 1984; Green, 1996; Watson, 1997) and so such opportunities for immatures are probably limited in this region and may encourage immatures fledged in western Scotland to move further afield. Ring recoveries suggest that this does happen (Grant and McGrady, 1999; Watson, 2002). Moreover, we have shown that the distribution of immatures was not associated with areas of high fledgling production but with the distribution of persecution, suggesting that some immatures moved away from their natal areas and congregated in areas where persecution was prevalent.

The association between former territories where persecution was prevalent and non-breeding immatures is understandable because the removal of territorial breeding birds by persecution creates suitable habitat that is undefended. In addition, because persecution is most common on grouse moors in eastern and central Scotland (Whitfield et al., 2003) where prey availability can be high (and much higher than in many parts of western Scotland, e.g., Watson et al., 1989, 1992), these

areas are probably extremely attractive to immatures. Since the attractiveness of these areas is created in part by a desire of grouse moor managers to prevent eagles from reducing red grouse stocks, the replacement of a pair of territorial eagles by up to several immature eagles is hardly a satisfactory outcome from this perspective. So it is not surprising that persecution of eagles continues, with immatures also being killed, as evidenced by repeated offences in the same areas, despite the difficulties in detecting them (e.g., RSPB, 1999, 2001). Unfortunately, this creates 'black holes' or 'ecological traps' for immature eagles (Grant and McGrady, 1999; Delibes et al., 2001) which, because of their attractiveness to mobile immatures, draw in birds from far afield, elevating immature mortality rates and adversely affecting population dynamics over a much wider area (Real and Mañosa, 1997; Watson, 1997). This process has been modelled by Delibes et al. (2001) which shows that it progressively erodes the floater section of the population without any apparent impact on the breeding population, which then declines very suddenly, creating an urgent need for remedial action, which is often difficult to carry out. It is of great concern, therefore, that the present study has identified features consistent with this process occurring in Scottish golden eagles as a result of persecution.

Our study indicates that persecution, mainly on grouse moors, may be adversely affecting all aspects of the population dynamics of golden eagles in Scotland. Of particular concern are: (1) the potential negative impacts on adult and immature survival, since these demographic parameters are most influential in affecting trends in eagle populations (e.g., Ferrer and Calderón, 1990; Green et al., 1996; Real and Mañosa, 1997), and (2) the several territorial vacancies associated with persecution on grouse moors. Although the total number of territories occupied by pairs of golden eagles in Scotland did not change between 1982 and 1992 (Green, 1996), our results suggest that such apparent stability may mask underlying problems: at worst the population may be at risk of decline, and at best persecution on grouse moors is probably preventing the population from realising its full geographical potential.

Watson and Whitfield (2002) recently presented a preliminary conservation framework for the golden eagle in Scotland that considered targets for 'favourable conservation status'. Kenward et al. (2000) have highlighted the importance of adult survival and the occurrence of non-breeding adult floaters as indicators of the long-term resilience of raptor populations to change (and, therefore, their 'status'), yet these attributes can be difficult to measure and potentially costly to monitor over large areas. However, the proportion of pairs that is adult is a readily recorded measure that (albeit imperfectly) reflects age of breeding and therefore, implicitly, is an indirect indicator of population status. The

targets for favourable conservation status presented by Watson and Whitfield (2002) did not include such a measure. Hence, echoing the approach advocated by Balbontín et al. (2003), we strongly suggest that an additional target for favourable status in a conservation framework for Scottish golden eagles should be that in at least 95% of pairs both partners are adults, reflecting the estimate of this parameter in persecution-free regions and in contrast to contemporary national estimates of 85–89%. Policies towards achieving this target and monitoring of progress should be directed at those grouse moor areas where persecution is greatest, especially since prevention of persecution would bring additional benefits to the population.

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