

Territorial behaviour of Golden Eagles in Western Norway



Gunnar Bergo

Like many raptors, the Golden Eagle *Aquila chrysaetos* has a regularly spaced population in traditional nesting areas (e.g. Dixon 1937; Brown 1976b; Gjershaug 1981; Tjernberg 1983; Bergo 1984a). For many species, this accords well with the idea that breeding density is limited by territorial behaviour (Newton 1979); territoriality is a means of maintaining exclusive use of resources in a limited area, and implies the defence of this area by its owner. A study in Idaho, USA, described the Golden Eagle as territorial (US Dept of the Interior 1979), but Brown

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(1976b) considered that this species lacked obvious territorial defence and he preferred to use the term 'home range' instead of 'territory', home range being the whole area used, but not necessarily defended, by the birds.

Golden Eagles are sparsely distributed, but regularly spaced within suitable habitats in the mountains of Scandinavia (Gjershaug 1981; Fremming 1982; Tjernberg 1983; Bergo 1984b). The aim of the present study was to describe and quantify Golden Eagle behaviour in nesting areas in an attempt to understand how regular nest-spacing is maintained.

Study area

The study was carried out in Hordaland (14,960 km²), Western Norway (fig. 1). In this region, 16% of the area is forest and 46% is mountains above the tree-line (Miljøstatistikk 1978). The study area itself was a series of narrow valleys in broken mountainous country in which pairs of breeding Golden Eagles were regularly spaced, with a mean distance to their nearest neighbour of 16 km (Bergo 1984a).

Three pairs (1-3) and a 'trio' of eagles were studied, with eyries, all in cliffs, in subalpine forest of birch *Betula odorata*, which here forms the tree-line at 600-900 m above sea level, and a fourth pair (4) with a nesting

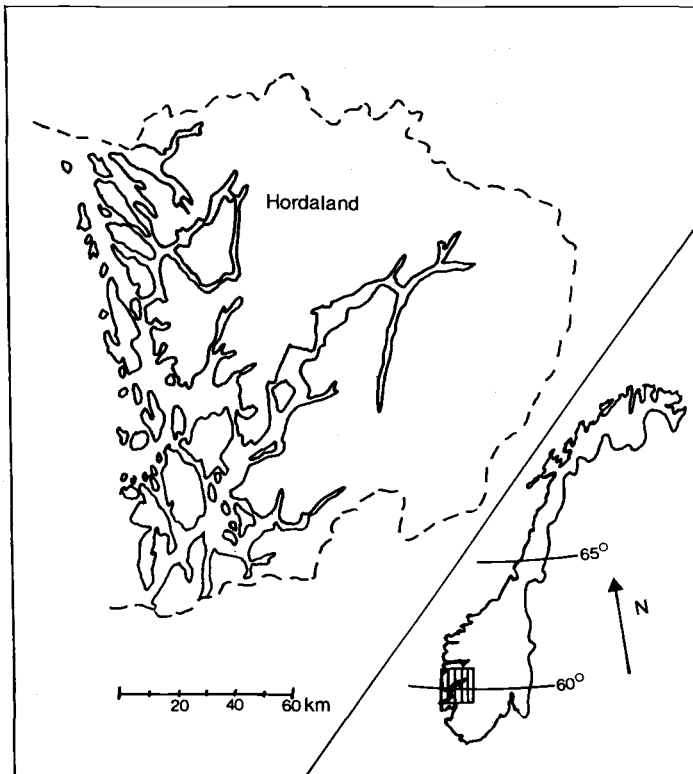


Fig. 1. Map of study area of Golden Eagles *Aquila chrysaetos* in Western Norway, 1981-83

area in the coastal region, an area of more-rounded hills covered with forest of Scots pine *Pinus sylvestris*.

The most common diurnal breeding bird partly exploiting the same resources as the Golden Eagle in this area was the Raven *Corvus corax*. Rough-legged Buzzards *Buteo lagopus* and Kestrels *Falco tinnunculus* are common when rodents are abundant, but were relatively scarce during the study period (1981-83). Gyrfalcons *F. rusticolus* bred only in small numbers in the inner mountains. White-tailed Eagles *Haliaeetus albicilla* had recently re-established themselves as breeders in the coastal region.

Methods

Table 1 details 496 hours of observations between March 1981 and April 1983. During the study, pairs 1 and 2 were breeding, while pairs 3 and 4 consisted of sub-adult eagles establishing territories. Data were collected throughout the year only for pair 1. All three birds in the 'trio' took part in all breeding activities, but only two were sexed with certainty.

Table 1. 'Observation minutes' (OM) and 'eagle minutes' (time during which eagle in view) (EM) in various periods of year during a study of Golden Eagles *Aquila chrysaetos* in Western Norway, 1981-83

See text for limits of each period of year. X = sex unknown.

Period	Pair 1 (1981)			Pair 2 (1982, 1983)			Pair 3 (1981)			Pair 4 (1981, 1982)			'Trio' (1982)			X
	OM	EM		OM	EM		OM	EM		OM	EM		OM	EM		
		♂	♀		♂	♀		♂	♀		♂	♀		♂	♀	
Pre-laying	990	136	222	440	81	161	770	126	119	1,560	203	229	1,080	91	155	194
Incubation	1,480	352	1,311	480	193	480	682	49	63	1,210	178	156	1,050	228	975	647
Nestling	5,400	389	2,621	865	98	702	450	57	52	510	148	128	5,080	326	3,914	1,853
Post-fledging	3,440	125	908	—	—	—	—	—	—	—	—	—	630	66	226	45
Autumn/winter	2,000	499	487	—	—	—	—	—	—	1,640	327	568	—	—	—	—
Total	13,310	1,501	5,549	1,785	372	1,343	1,902	232	234	4,920	856	1,081	7,840	711	5,270	2,739

The pairs and the 'trio' were not neighbours; they were chosen for study because of the visibility and accessibility of their nesting areas and because the individual eagles concerned (apart from one) could be sexed readily. Observations were confined to activities within the 'core area' of each home range, which varied from 10km² to 35km² and excluded the greater part of each pair's hunting range. A standardised system of recording was used, following the activity classes defined below. Systematic observations were made between 06.00 and 18.00 hours and averaged five hours in length; random observations were made at other times. To minimise errors, each sample period was two hours or more in duration.

Eagles were divided into two age classes: sub-adult (white feathers in wings and/or tail), and adult (no white markings). Sex determination was based on size difference and behaviour during copulation and laying. Each year was divided into five periods: pre-laying (about 20th February to 20th March); incubation (about 21st March to 5th May); nestling (about 6th May to 20th July); post-fledging (about 21st July to 1st October); and autumn/winter (about 2nd October to 19th February).

Behaviour was classified as follows:

Aerial: Soaring flight; Slow gliding flight (including 'hanging on the wind'); Fast gliding flight; Flapping flight; Diving; and Undulating flight (in which a 'wave' was the distance from one peak to the next, see fig. 2; and a continuous series was termed a 'sequence').

'High aerial' activities were flights performed above topographic features such as hills and mountains, while 'low aerial' activities were flights performed inconspicuously inside valleys etc.

Perching (see fig. 3): Exposed perching (use of the highest and most exposed perch, giving optimal view, with no shelter); Conspicuous perching (good, but not optimal, view; only moderate shelter); Inconspicuous perching (restricted view, good shelter).

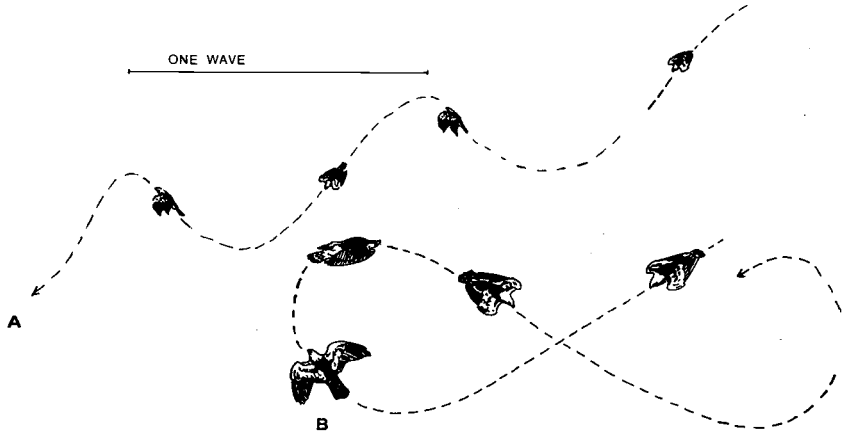


Fig. 2. Pattern of Undulating flights of Golden Eagles *Aquila chrysaetos*. A: eagle dives with wings partly closed, then regains height, sometimes with vigorous wing-flapping; this is repeated. B: a special form of Undulating flight is the 'Pendulum flight' in which eagle dives, regains height, and turns over and retraces its course repeatedly. (Drawing by R. Roalkvam)

Results

Eagles were in view for 66.8% of the total observation time, and when not at the nest were mainly seen flying.

Aerial behaviour

Aerial behaviour is summarised in fig. 4. Slow gliding and Soaring flight were the main activities (78-89%). The eagles soared on upslope winds and on thermals to gain height before gliding off towards hunting areas, and Slow gliding was also used to gain height along slopes and cliffs. When hunting from the air, they were mainly Slow gliding (see Bergo 1983). On three occasions, approaching an intraspecific intruder, resident eagles performed Flapping flight with an emphasised downstroke; this behaviour was also observed when the female of pair 4 was approaching and chasing White-tailed Eagles.

The Golden Eagles usually made very conspicuous and long dives to their eyries, and Undulating flight was twice observed at the start of these dives. Undulating flight was performed with some variation: true 'Pendulum flight' by the female of the 'trio' was observed twice, but the eagles usually performed flights intermediate between types A and B (see fig. 2). Resident eagles performed Undulating flight in six of eight cases

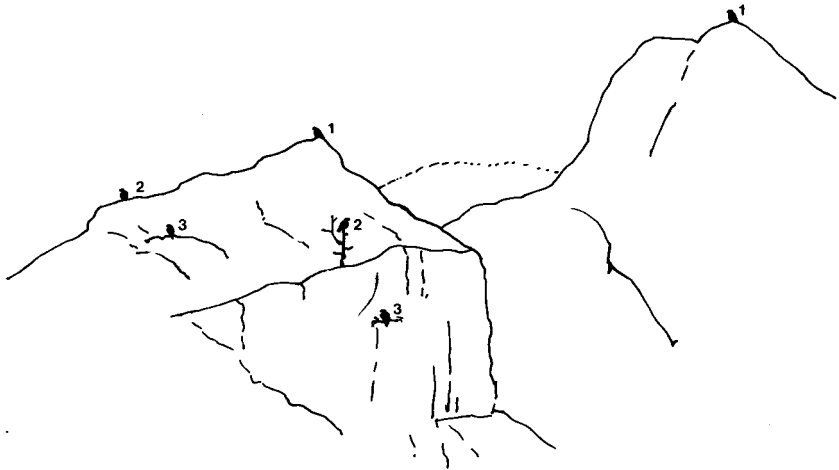


Fig. 3. Types of perching behaviour used by Golden Eagles *Aquila chrysaetos*, 1: Exposed perching, 2: Conspicuous perching, 3: Inconspicuous perching (Drawing by R. Roalkvam)

where intraspecific intruders appeared in the core areas; in the two cases with no such response, the eagles were on the ground in calm weather. In 22 of 28 sequences of Undulating flight, the performer's mate was in the core area and probably within sight. Of 39 observed Undulating flights, 23 (59%) were within 1 km of the nest, 13 (33.3%) between 1 km and 2 km and three (7.7%) more than 2 km from the nest; 21 (53.8%) of the flights were classified as high aerial. Most Undulating flights were performed by females (table 2), but males had a 2.7 times higher frequency (Undulating flights/minutes eagles in view). Females performed Undulating flights with a greater number of waves per flight than did males, but the difference was not significant (t-test, $t = 1.91$).

Nine instances of 'mock attack and evasion routine' between partners were observed. In these, one of the eagles made a dive at the other, which then turned half over and presented its talons. Males attacked twice as often as females, and six of these 'attacks' were made by establishing eagles. Seven of nine registered mock attacks were classified as low aerial. Fledged eaglets (from pair 1 and the 'trio') were also observed making such attacks on their parents.

Table 2. Number of Undulating flights, and number of 'waves' per flight of Golden Eagles *Aquila chrysaetos* in study in Western Norway, 1981-83

	Males	Females
No. of Undulating flights	16	23
Mean no. of 'waves' per flight	3.8	6.1
Range	2-8	2-20

Perching behaviour

Perching behaviour is summarised in fig. 5. During the nestling period, the males of pairs 1 and 2 and of the 'trio' perched 'conspicuously' relatively more than did their female partners. At other periods, there appeared to be no such difference between the sexes. (Table 1)

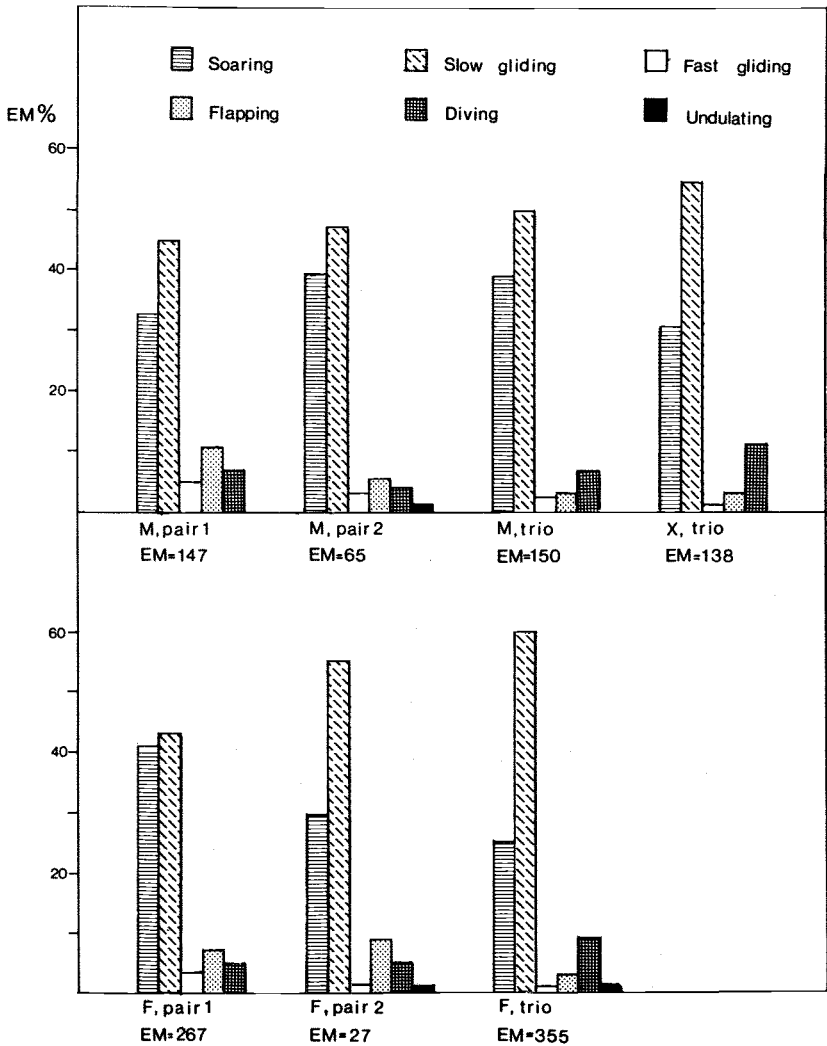


Fig. 4. Flight behaviour (as percentages of 'eagle minutes', EM) of Golden Eagle *Aquila chrysaetos* pairs 1, 2 and the 'trio' during nestling period. M = male; F = female; X = sex unknown

Exposed perching was observed on only five occasions. In two instances, the reasons were unclear. In another, it may have been in response to a passing intruder, and in the fourth case it was adopted by a sub-adult male while his partner inspected a traditional nest site. In the fifth instance, a female adopted Exposed perching for about half an hour in the pre-laying period, before she was joined by her mate and copulation took place. Of six other observed copulations, four were performed on Conspicuous perches and two on Inconspicuous ones.

Of a total of 47 perches used by pair 1, two were Exposed, ten were Conspicuous and 35 were Inconspicuous. The eagles preferred perches

Table 3. Characteristics of perches used by Golden Eagle *Aquila chrysaetos* pair 1 in breeding season, Western Norway, 1981-83

Total number of perches used was 47. Total number of grid points was 321 (see Mysterud 1983). Under 'Preference', values above 0.15 express a positive preference

	No. perches	Grid points	Preference
DISTANCE TO NEST			
<100 m	10	2	5.00
100-1000 m	12	33	0.36
> 1000 m	25	286	0.09
ELEVATION OF PERCH			
Below nest	5	105	0.05
At nest height	3	12	0.25
Above nest			
<200 m	27	81	0.33
>200 m	12	123	0.10
VIEW OF NEST			
Good	37	74	0.50
Limited	7	63	0.11
None	3	184	0.02

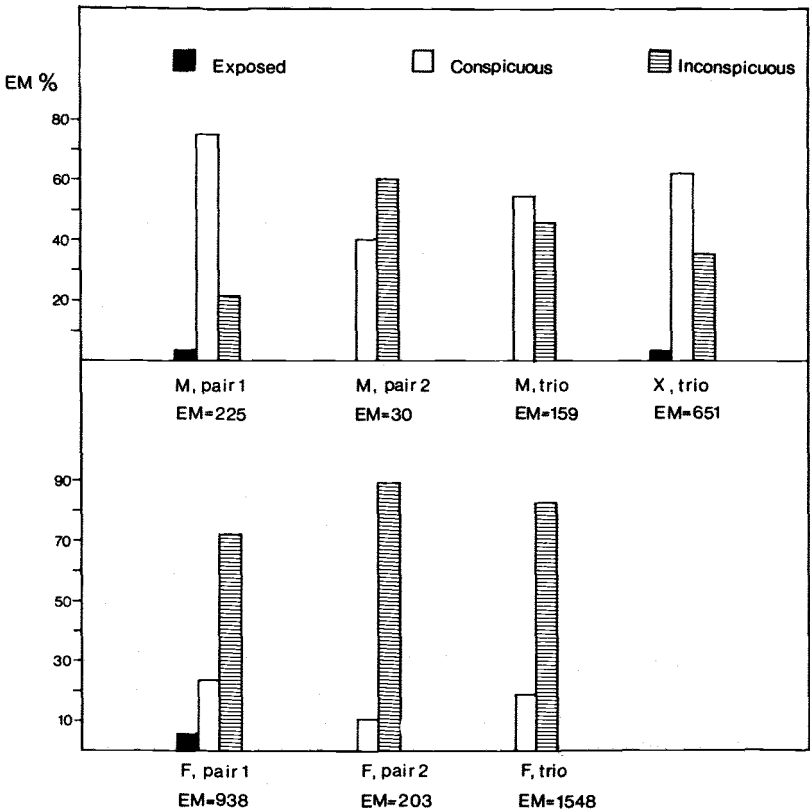


Fig. 5. Perching behaviour (as percentages of 'eagle minutes', EM) of Golden Eagle *Aquila chrysaetos* pairs 1, 2 and the 'trio' during nesting period. M = male; F = female; X = sex unknown

situated relatively close to and somewhat higher than their nest, giving a good view of it (table 3). The sexes each had their own favourite perches near the nest, although these were also used by both members of the pair.

Behaviour at the nest

Both sexes took part in nest-building, which was most frequently observed in the pre-laying period. In addition to nest-building, the eagles decorated their nests with 'greenery'. The frequency with which breeding eagles brought greenery to their nests was similar during pre-laying, incubation and nestling periods (table 4). In the nestling period, most greenery was delivered by females*. Pair 4 also brought greenery to an alternative nest in the pre-laying period. In one nestling period (June 1982), the three eagles of the 'trio' built two new nests and added new sticks to their 1981 nests while their eaglet was still in the active nest.

Table 4. Deliveries of greenery to nests by breeding Golden Eagles *Aquila chrysaetos* (pairs 1, 2 and 'trio') in pre-laying, incubation and nestling periods, during study in Western Norway, 1981-83

	Frequency = deliveries/observation minutes $\times 10^4$					
	PERIOD					
	Pre-laying		Incubation		Nestling	
	♂	♀	♂	♀	♂	♀
No. of deliveries	3	4	3	3	4	23
Frequency	12	16	10	10	3.5	20.3

Both sexes participated in the breeding duties. The females did 65-99% of incubation and care of the young, while the males did most of the hunting. In the first two weeks of the nestling period, females spent nearly all their time on the nest or in its close vicinity. As the eaglets grew, the females grew less attentive and began participating in hunting. Only females were seen to stay on the nest overnight.

Vocal behaviour

Because the eagles were usually distant, it is probable that not all calls were registered. Calls were, however, heard in three different types of situation: (i) during incubation, all the breeding females were heard to call from the eyrie when they sighted males returning with prey; (ii) the female of pair 4 once called loudly when an intruder came close to the nest; and (iii) both the female and the male of pair 4 were vocal during nest-building.

Seasonal variation in behaviour

The eagles were seen in their nesting areas at all times of the year (table 1). During autumn/winter, pairs 1 and 4 were seen in 78% and 100% respectively of all observations of more than two hours' duration ($n = 15$). The relative proportions of time spent by pair 1 in flight and in perching behaviour varied throughout the year (table 5): during autumn/winter and before laying, both sexes perched for most of the day, but aerial activity increased as breeding approached; during incubation, the female was recorded on the nest for 88.6% of the total time she was in view; during the

* χ^2 13.37, $P < 0.001$

Table 5. Distribution of main activities of Golden Eagle *Aquila chrysaetos* pair 1 in various periods, as percentage of total minutes eagles in view, based on study in Western Norway, 1981-83

Activity	PERIOD									
	Pre-laying		Incubation		Nestling		Post-fledging		Autumn/winter	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Aerial	27.1	24.0	15.3	3.4	37.8	10.2	37.0	14.1	8.0	18.7
Perching	72.0	72.6	17.4	8.0	57.8	35.8	63.0	85.9	92.0	81.3
On nest	0.9	3.4	67.3	88.6	4.4	54.0	0	0	0	0
Total	100	100	100	100	100	100	100	100	100	100

nestling period, the male was observed in the core area for only about 7% of the total observation time, and was on the nest for short visits only; in the post-fledging period, the female was seen perched relatively more often than the male.

Undulating flight was performed at all times of the year (table 6), but 1.5 times more frequently in the pre-laying period than the average. There was, however, considerable variation between individuals.

Both pairs 1 and 4 spent most time together during the autumn/winter and the pre-laying periods (table 7). Pair 4 (establishing eagles) spent relatively more time together than pair 1 (breeding).

Table 6. Number of Undulating flight sequences by Golden Eagles *Aquila chrysaetos* in relation to time of year, during study in Western Norway, 1981-83

Period	Pair 1		Pair 2		Pair 3		Pair 4		'Trio'			Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	x	♂	♀
Pre-laying	0	0	1	0	1	2	1	1	1	0	1	4	3
Incubation	2	0	0	0	1	0	0	2	0	0	0	3	2
Nestling	0	0	1	1	0	0	2	5	0	2	0	3	8
Post-fledging	0	0	—	—	—	—	—	—	1	1	1	1	1
Autumn/winter	1	1	—	—	—	—	0	1	—	—	—	1	2

Table 7. Time spent together by breeding pair of Golden Eagles *Aquila chrysaetos* (pair 1) and establishing pair (pair 4) in various periods, expressed as percentage of total minutes eagles in view

Aerial = flying in same direction, within a few metres; Perching = <1 m apart

Period	PAIR 1			PAIR 4		
	Aerial	Perching	Total	Aerial	Perching	Total
Pre-laying	1.4	0.3	1.7	19.8	0.9	20.7
Incubation	0	0.4	0.4	12.4	5.4	17.8
Nestling	0.4	0.1	0.5	22.7	4.1	26.8
Post-fledging	0.7	0	0.7	—	—	—
Autumn/winter	3	11.8	14.8	0.2	26.7	26.9
Mean %	1.1	2.5	3.6	13.8	9.3	23.1

Intraspecific confrontations

During 496 hours of observations, eight intruders (all sub-adult) were observed within the five core areas (table 8). No encounters between neighbours were seen. Intruders were observed 3.5 times more frequently in the core areas of establishing eagles than in those of breeding eagles, and most frequently in the pre-laying and autumn/winter periods.

Table 8. Number and relative appearance of intruding Golden Eagles *Aquila chrysaetos* in core areas of home ranges of other Golden Eagles in various periods of year, Western Norway, 1981-83

	Relative appearance = intruders/observation minutes $\times 10^4$				
	Pre-laying	Incubation	Nestling	Post-fledging	Autumn/winter
No. of intruders	4	1	1	0	2
Relative appearance	8.3	2.1	0.8	0	5.5

Within the core areas, females tended to be more involved than males in aggressive encounters. On two occasions in the pre-laying period, there were conflicts between the female of pair 4 and an intruder only a few metres from the eyrie (one of the intruders was probably a female, the other could not be sexed); the resident female was very 'upset' and called loudly during the intrusions. On both occasions, the resident male was in the area, but did not appear to respond.

In the nestling period, the female of the 'trio' (who was alone in the area) performed Undulating flight directly from the eyrie, approaching an intruder. For some minutes, she chased the intruder, which in turn began mobbing her when she was at a lower height. About half an hour later, the intruder was driven away, and the female performed Undulating flight before assuming Conspicuous perching, close to her eyrie. During incubation, the female and male of pair 3 were seen chasing an intruder out of the core area more than 3km from the eyrie. One of the resident eagles (probably the male) dived menacingly towards the intruder, which turned around, presenting its talons. When the resident eagles returned, the male performed Undulating flight above the nesting cliff. Of the intruders recorded, four were not chased by the resident eagles, although on at least two occasions Undulating flights were performed in apparent response.

Interspecific confrontations

The resident eagles usually ignored other bird species within the core area, but confrontations were nevertheless frequent. Males were involved 2.5 times as often as females, although females were involved in most episodes (table 9). Interspecific confrontations were recorded 2.1 times more frequently in the core areas of the establishing eagles (pairs 3 and 4) than in the core areas of the breeding eagles. Aggressive encounters (hunting excluded) were initiated by the intruders in 46 (78%) of 59 recorded cases.

In 1981, a pair of White-tailed Eagles built a nest about 250m from the nest of pair 4. This caused much aggression, initiated by the Golden Eagles (and the female in particular) on eight out of ten occasions. The White-tailed Eagles deserted at the start of the incubation period.

The shortest recorded distances to occupied nests of other potential competitors were: Raven 0.5km, Gyrfalcon 3.5km and Rough-legged Buzzard 4km.

Discussion

A territory may be maintained by actual defence (attacking/chasing intruder) and by identifying-acts, such as calls and various displays (see Brown & Orians 1970). A small, intensively used area is often defended

Table 9. Number of confrontations between other bird species and Golden Eagles *Aquila chrysaetos* in their home range core areas, Western Norway, 1981-83

Based on 3,672 minutes' observation of males, and 13,477 minutes' observation of females

Other species	MALES			FEMALES		
	Number confrontations	Eagle chasing	Eagle mobbed	Number of confrontations	Eagle chasing	Eagle mobbed
Raven <i>Corvus corax</i>	9	2	8	8	3	7
Kestrel <i>Falco tinnunculus</i>	4	0	4	10	0	10
White-tailed Eagle <i>Haliaeetus albicilla</i>	3	2	2	6	6	4
Carrion Crow <i>Corvus corone</i>	4	0	4	3	0	3
Rough-legged Buzzard <i>Buteo lagopus</i>	1	1	1	2	1	1
Common Gull <i>Larus canus</i>	2	0	2	1	0	1
Fieldfare <i>Turdus pilaris</i>	0	0	0	2	0	2
Goshawk <i>Accipiter gentilis</i>	0	0	0	1	0	1
Buzzard <i>Buteo buteo</i>	1	0	1	0	0	0
Merlin <i>Falco columbarius</i>	0	0	0	1	0	1
Short-eared Owl <i>Asio flammeus</i>	0	0	0	1	0	1
Total	24	5	22	35	10	31

totally, but where eagles range over a larger area it tends to be less exclusive (Newton 1979). Various behavioural activities may advertise occupancy. For several species of raptor, Exposed perching and aerial displays, such as Soaring and Undulating flight, have been interpreted as forms of advertisement (Brown & Amadon 1968; Gargett 1975; Weir & Picozzi 1975). Visual signals are no doubt the most effective over relatively long distances for raptors breeding in open habitats.

Territorial behaviour by the Golden Eagle

Golden Eagles in a thinly distributed breeding population like that in Western Norway probably have little need to defend their entire home range in a strictly territorial manner, which would in any case be very costly in terms of expended energy. Visual advertisement clearly works over long distances, and, according to Schlaer (1972), Golden Eagles are able to see details 2.4 to 2.9 times as fine as can human beings. This implies that Golden Eagles can see each other at a range of at least 6 km when in the air.

Aerial behaviour was probably over-represented in the present study, since the eagles were most often spotted when flying. Slow gliding and Soaring were seen most frequently. Travelling and hunting seemed to be the main functions of Slow gliding flight, but any high aerial activity (including 'hanging on the wind') may also have the effect of advertisement. Soaring was used primarily to gain height before travelling to hunting areas. Carnie (1954) regarded Soaring as a part of the eagles' main hunting technique, but no hunting was recorded from Soaring flight during this study (Bergo 1983). As suggested by Brown (1976b), Soaring probably functions as advertisement in addition to its primary function of gaining height.

When approaching intruders such as White-tailed or other Golden Eagles, the resident bird usually emphasised the downstroke of the wingbeat as described for the Buzzard *Buteo buteo* (Weir & Picozzi 1975),

probably as a form of threat. The marked and long dives to the eyries may have a sexual function, but could also serve as advertisement.

The Golden Eagles' most spectacular aerial behaviour was undoubtedly the Undulating flight, which has been interpreted as sexually motivated behaviour (e.g. Bent 1937; M. J. Everett in preparation). Brown (1976a) described Undulating flight as an advertisement display, but noted that females also performed it in the presence of their mates. Undulating flight has also been recorded for nearly all other large eagles (Brown 1976a). In the USA, Harmata (1982) found that in 73% of the cases the appearance of intruders resulted in Undulating flight by the resident Golden Eagle, and he proposed that this was primarily a territorial and threat display. This accords well with the observations in the present study, although Undulating flight was also performed at lower altitudes, seemingly without intruders in the area, and thus may have had a sexual function, too.

Mock attack and evasion routine by pairs of Golden Eagles have been recorded by several authors (Gordon 1955; Ross 1941; Brown 1976b), and were observed during this study. Brown (1976b) considered that they may have involved a symbolic food-pass, but, as food-passes are seldom recorded for the Golden Eagle, and as females also were observed to 'attack', this explanation is probably not valid. The behaviour resembles the fighting 'routine' in direct conflicts between eagles, and probably also functions as sexual behaviour when performed between mates.

In densely breeding populations of Verreaux's Eagles *Aquila verreauxii* and Buzzards, Conspicuous perching and High perching were considered to be territorial advertisement (Gargett 1975; Weir & Picozzi 1975, 1983). This form of advertisement is probably unimportant for sparsely distributed Golden Eagles in Western Norway, where their habit of Conspicuous and Inconspicuous perching indicated that perches giving some form of shelter might be more important. In the central parts of the core area, Golden Eagles probably select perches giving a good view of the nest, while in more remote parts hunting may influence their perching behaviour. The males' tendency to perch more Conspicuously than females in the nestling period can probably be explained simply by the females' stronger attachment to the nest.

Like many other raptors, Golden Eagles bring green plant material to their nests (Gordon 1955; Brown 1976b; Gjershaug 1981; Fremming 1982). Gjershaug (1981) concluded that this habit might have several functions and suggested that one might be to camouflage the nest. Fremming (1982) emphasised the marked visual effect of greenery on an otherwise brown-coloured nest, and Newton (1979) suggested that the greenery might be a form of advertisement over a shorter range, serving to denote an occupied territory. The present study showed that greenery may be brought to the nests, occupied or not, at all times of the year, but most regularly by the female in the nestling period. Newton's (1979) explanation is probably the best, but he did also point out that a primary purpose in advertisement does not exclude the possibility of other subsidiary functions. Starlings *Sturnus vulgaris* also furnish occupied nestboxes with one or a few green twigs (J. Karlsson *in litt.*).

Calling may have a threat function (Linsenmair 1971), and several diurnal raptors—for example, White-tailed Eagle (Willgoos 1961), Imperial Eagle *A. heliaca* (Meyburg 1975) and Verreaux's Eagle (Gargett 1975)—are reported to be vocal when disturbed by an intruder. The Golden Eagle, however, is apparently much less vocal, and probably uses its voice less than any other West Palearctic *Aquila* (Cramp & Simmons 1980). The relatively open habitat and large distances between neighbours make it unlikely that Golden Eagles use vocal signals in advertising their nesting areas in Western Norway.

In the USA, Craighead (1967) and Camenzind (1969) reported breeding eagles calling when disturbed at the nest by human beings. This has never been reported in Scandinavia, but in this study the female of pair 4 was heard calling loudly when disturbed by another, intruding, Golden Eagle. Apart from some calling between the mates, such as the female's food-begging call (see Dixon 1937), the 'threatening' call was the only call heard during this study.

In Western Norway, Golden Eagles probably maintain their territories basically by their presence and daily activities throughout the year. This was also found to be the case with the related Australian Wedge-tailed Eagle *A. audax* (Brooker 1974). No particular period seemed to be used for advertising, but the limited aerial activity of pair 1 in winter suggested a low level of advertisement. High aerial activities are probably related more to atmospheric conditions than to time of year, as also indicated in the case of the Wedge-tailed Eagle (Brooker 1974).

Intraspecific and interspecific confrontations

In the very dense breeding population of Verreaux's Eagles in Zimbabwe, Gargett (1975) recorded 89 encounters between neighbours, of which only five were aggressive, while 185 aggressive encounters between resident eagles and 'floaters' were generally of longer duration than those between neighbours. In a sparse population of Wedge-tailed Eagles in Australia, only a few observations were made of residents chasing intruders (Brooker 1974).

Haller (1982) recorded relatively many aggressive encounters in a sparse population of Golden Eagles in the central Alps, but found that neighbours were chased shorter distances than other intruders. In Møre and Romsdal, northwestern Norway, Gjershaug (*in litt.*) observed a five-minute confrontation between neighbouring Golden Eagles, involving Undulating flight and calling, probably following a 'border violation'; the eagles bred only 3 km apart, while mean distance to nearest neighbour in the population was 14.7 km (Gjershaug 1981).

No encounters between neighbours were recorded in the present study, and only eight conspecific intruders were observed in the core areas. This probably reflects the sparseness of the population in the area (Bergo 1984a), which also means that encounters would be expected to occur in the peripheral parts of home ranges. In the breeding season, such encounters are most likely between males, the females being close to the nest for most of the time.

The increase in intrusions by immature or sub-adult eagles in the pre-laying and autumn/winter periods may be a consequence of more active searching for mates and potential nesting areas at these times of year. Gargett (1975) also registered more contacts between Verreaux's Eagles in these periods, while, according to Haller (1982), these were the only periods when Golden Eagles in the central Alps actually injured each other in fights. The results of the present study indicate that eagles establishing themselves in nesting areas advertise their presence more intensively than do established breeding pairs. Gargett (1975) and Haller (1982) reached similar conclusions.

Most aggressive encounters described by other authors involved intruders and resident eagles of the same sex, with less aggression between eagles of opposite sexes (e.g. Lochart, Ellis & Harmata in Harmata 1982). This was also indicated by the observations made during this study. Eagles of the same sex are possibly regarded as a more serious threat and as potential rivals.

It is well known that birds of prey are regularly subjected to mobbing by other birds, even those which may be potential prey. In the study area, Ravens were the most frequent mobbers, but Golden Eagles were also observed chasing Ravens. More-serious confrontations may occur between different raptor species. In Africa, Tarboton (1977) reported breeding failure of Wahlberg's Eagle *A. wahlbergi* as probably a result of continuous harassment by Black-shouldered Kites *Elanus caeruleus*, while in France Cheylan (1973) reported that Golden Eagles and Bonelli's Eagles *Hieraetus fasciatus* were mutually exclusive in distribution and defended their nesting areas against each other. In the present study, a pair of White-tailed Eagles failed to breed perhaps as a result of the aggressiveness of the neighbouring Golden Eagles. Willgohs (1961) gave examples of similar conflicts between these species in which Golden Eagles appeared to be dominant.

In the Scottish Highlands, Golden Eagles breed in the same habitats as Peregrines *Falco peregrinus* and Ravens, and wherever the breeding density of the eagle is high, densities of Peregrine and Raven are low, and *vice versa* (Ratcliffe 1962). Ratcliffe (1962) suggested that this may be a result of competition, but regarded the Golden Eagle as the dominant species. In Western Norway, Ravens seemed to avoid breeding close to Golden Eagles, but the species might be competing for carcasses. Competition for food with the Gyrfalcon may also occur in some areas (Gjershaug 1981). Of all specifically distinct competitors, however, probably only human beings have an important influence on the spacing of Golden Eagles in Western Norway (see Bergo 1984a).

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Summary

The behaviour of Golden Eagles *Aquila chrysaetos* in five nesting areas in Western Norway was studied during 1981-83 and related to territorial advertisement and pair spacing. Aerial activities, perching, behaviour at the nest, and relations with other Golden Eagles and other species are described. Soaring, 'hanging on the wind' and Undulating flight may all act as territorial advertisement signals, and the possibility of long dives to the nest and nest-decoration with greenery having similar functions is discussed. Exposed perching and calling are probably not involved in advertisement behaviour in this sparse breeding population.

References

- BENT, A. C. 1937. *Life Histories of North American Birds of Prey*. US Nat. Mus. Bull. 167.
- BERGO, G. 1983. Jaktatferd hos kongeørn. *Fauna* 36: 125-128.
- 1984a. Population size, spacing and age structure of Golden Eagle *Aquila chrysaetos* (L.) in Hordaland, West Norway. *Fauna norv. ser. c. Cinclus* 7: 106-108.
- 1984b. Habitat and nest-site features of Golden Eagle *Aquila chrysaetos* (L.) in Hordaland, West Norway. *Fauna norv. ser. c. Cinclus* 7: 109-113.
- BROOKER, M. G. 1974. Field observations of the behaviour of the Wedge-tailed Eagle. *Emu* 74: 39-42.
- BROWN, J. L., & ORIANS, G. H. 1970. Spacing patterns in mobile animals. *A. Rev. Ecol. Syst.* 1: 239-262.
- BROWN, L. H. 1976a. *Eagles of the World*. Newton Abbot.
- 1976b. *British Birds of Prey*. London.
- & AMADON, D. 1968. *Eagles, Hawks and Falcons of the World*. London
- CAMENZIND, F. J. 1969. Nesting ecology and behaviour of the Golden Eagle *Aquila chrysaetos* L. *Brigham Young Univ. Sci. Bull. Biol. ser.* 10: 4-15.
- CARNIE, S. K. 1954. Food habits of nesting Golden Eagles in the coast ranges of California. *Condor* 56: 3-12.
- CHEYLAN, G. 1973. Note sur la compétition entre l'Aigle royal *Aquila chrysaetos* et l'Aigle de Bonelli *Hieraetus fasciatus*. *Alauda* 41: 303-312.
- CRAIGHEAD, J. 1967. Sharing the lives of wild Golden Eagles. *Nat. Geogr. Mag.* 132: 420-439.
- CRAMP, S., & SIMMONS, K. E. L. (eds.) 1980. *The Birds of the Western Palearctic*. vol. 2. Oxford.
- DIXON, J. B. 1937. The Golden Eagle in San Diego County, California. *Condor* 39: 49-56.
- FREMMING, O. R. 1982. Reproduksjonsøkologi hos kongeørn *Aquila chrysaetos* (L.) i et fjellkjedeområde i Sør Norge. Thesis, University of Oslo.
- GARGETT, V. 1975. The spacing of Black Eagles in Matopos, Rhodesia. *Ostrich* 46: 1-44.
- GJERSHAUG, J. O. 1981. Hekkeøkologi hos kongeørn *Aquila chrysaetos* (L.) i Møre og Romsdal. Thesis, University of Trondheim.
- GORDON, S. 1955. *The Golden Eagle, King of Birds*. London.
- HALLER, H. 1982. Raumorganisation und Dynamik einer Population des Steinadlers *Aquila chrysaetos* in den Zentralalpen. *Orn. Beob.* 79: 163-211.
- HARMATA, A. R. 1982. What is the function of undulating flight display in Golden Eagles? *Raptor Research* 16: 103-109.
- LINSENMAIR, K. E. 1971. *Hvorfor synger fuglene?* Oslo.
- MEYBURG, B.-U. 1975. On the biology of the Spanish Imperial Eagle *Aquila heliaca adalberti*. *Ardeola* 21: 245-283.
- MILJØSTATISTIKK. 1978. *Statistiske analyser nr. 37*. Statist. Sentralbyrå, Oslo.
- MYSTERUD, I. 1983. Characteristics of summer beds of European brown bears in Norway. *Int. Conf. Bear Res. and Manage.* 5.
- NEWTON, I. 1979. *Population Ecology of Raptors*. Berkhamsted.
- RATCLIFFE, D. A. 1962. Breeding density in the Peregrine *Falco peregrinus* and Raven *Corvus corax*. *Ibis* 104: 13-39.
- ROSS, W. M. 1941. Aerial display by a pair of Golden Eagles. *Brit. Birds* 35: 82-83.
- SCHLAER, R. 1972. An eagle's eye: quality of the retinal image. *Science* 176: 920-922.
- TARBOTON, W. 1977. Nesting, territoriality and food habits of Wahlberg's Eagle. *Bokmakierie* 29: 46-50.
- TJERNBERG, M. 1983. Population density of Golden Eagle in relation to nest-site and food availability. In TJERNBERG, M., Breeding ecology of the Golden Eagle, *Aquila chrysaetos* (L.), in Sweden. Sveriges landbruksuniversitet. Rapport 10, Uppsala.

- US DEPT OF THE INTERIOR. 1979. *Snake River Birds of Prey: special research report*. Bureau of Land Management, Boise District, ID.
- WEIR, D., & PICOZZI, N. 1975. Aspects of social behaviour in the Buzzard. *Brit. Birds* 68: 125-141.
- & — 1983. Dispersion of Buzzards in Speyside. *Brit. Birds* 76: 66-78.
- WILLGOHS, J. F. 1961. The White-tailed Eagle *Haliaeetus albicilla albicilla* (L.) in Norway. *Arb. Univ. Bergen, Mat.: Nat. vid. ser.* 12: 1-222.

Gunnar Bergo, Department of Animal Ecology, Zoological Museum, University of Bergen, N-5000 Bergen, Norway