

Should Golden Eagles *Aquila chrysaetos* be Food Generalists or Specialists?

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ABSTRACT

Golden Eagles breeding in western Scotland take a wider range of prey than birds in eastern Scotland where the principal food comprises grouse and hares, and also breed less successfully. An analysis of trophic diversity was done for Golden Eagles from over 40 accounts in the literature. Birds in North America had the most restricted diets with birds in western Scotland amongst the most generalised while eagles in continental Europe were intermediate. As a rule, breeding performance was best where the diet was specialised and birds were able to concentrate on prey from just two or three taxonomic 'families'. This is believed to be linked to hunting behaviour. Hunting may be more efficient where a few types of appropriately sized prey animals are particularly abundant. In western Scotland, medium-sized herbivores (grouse and hares) have declined as numbers of larger grazing animals (sheep and deer) have greatly increased. Nowadays no naturally occurring animals in the Golden Eagle's preferred size range are especially abundant. Consequently eagles have been forced to take a wider spectrum of prey.

INTRODUCTION

During work on Golden Eagles *Aquila chrysaetos* and land use in the Scottish Highlands I was struck by the extraordinary variety of food brought to nests in parts of the western Highlands compared to the east. It was not unusual to find 10 or 15 different species amongst prey remains during a single visit to a west Highland eyrie. These included birds such as waders, ducks, seabirds, crows and grouse as well as mammals such as mice/voles, mustelids, lagomorphs and young ungulates. By contrast nearly all food at nests in the east Highlands was grouse (either Red Grouse *Lagopus lagopus* or Ptarmigan *Lagopus mutus*) or Mountain Hares *Lepus timidus*. At the same time there was a consistent tendency for birds in the east Highlands to breed

more successfully than eagles living in the west. This finding prompted the question 'Are eagles which exhibit a generalised diet living in less than optimal habitat ?'

METHODS

Information on the diet of Golden Eagles in Scotland was gathered during the breeding seasons of 1982-85. Food data were obtained from nest and roost sites at a range of localities across Scotland, three on the islands off the west coast, five on the west mainland and one in eastern Scotland (see Watson *et al.* 1993). Diet was assessed by analysis of regurgitated food pellets from which prey items were generally identified to the taxonomic 'family'. The breadth of the feeding niche was calculated, based on proportions in different families, using Levins (1968) formula:

$$B = 1 \sum p_i^2$$

where p_i represents the proportion of the diet contributed by the i th taxon. Values of this index range from 1 to n with larger values indicating a broader diet.

For eight of the nine localities information was also available on breeding success during most or all of the years 1982-85. An index of breeding success was calculated by taking the average nesting success over the study years for samples of typically between 10 and 20 pairs of eagles from each locality. Success was defined as the number of young fledged per pair of eagles.

Examination of the literature on Golden Eagles revealed equivalent information from a range of studies in North America and continental Europe. In some studies only data on diet were available and in others both diet and breeding success were reported. Where appropriate these results were used to extend the findings from Scotland.

RESULTS

Niche Breadth

The breadth of the feeding niche, or trophic diversity, was much higher amongst eagles in western Scotland than in the single eastern locality (Table 1). For studies elsewhere the range of trophic diversity measures was comparable to that found across Scotland. Consistently low figures were found amongst North American studies with values close to that for eastern Scotland (Table 2). Over much of continental Europe trophic diversity was lower than in western Scotland but higher than for much of North America (Table 3). Across the world range of the Golden Eagle there are four 'families' of prey animals which tend to be favoured, at least during the breeding season.

These are the rabbits and hares *Leporidae*, squirrels and marmots *Sciuridae*, grouse *Tetraonidae*, and pheasants *Phasianidae*. When the proportion of one or more of these families in the diet is high then trophic diversity tends to be low, and conversely when these families comprise little of the diet then diversity is high (Figure 1). Two conspicuous exceptions to this general rule occurred in the literature. On the island of Gotland in Sweden Golden Eagles showed a unique dependence on hedgehogs *Erinaceidae* and in Macedonia they specialised on tortoises *Testudinidae*. Dependence on the latter probably occurs more widely in SE Europe and the Middle East although as yet few studies of diet have been published from that region (Bahat, 1989).

Breeding Success.

Data on breeding success were available for more than half of the studies of diet. These confirmed a significant negative correlation between breeding success and trophic diversity ($r = -0.675$; $P < 0.001$). Where Golden Eagles had a narrow feeding niche they tended to breed more successfully than in localities where the feeding niche was broad (Figure 2).

DISCUSSION

Two clear patterns emerge from this review of feeding niche breadth and breeding success amongst Golden Eagles. When one or more of the families *Leporidae*, *Sciuridae*, *Tetraonidae* or *Phasianidae* make up a

Figure 1: Relationship between trophic diversity and the % of 4 principal prey taxa (Leporidae, Sciuridae, Tetraonidae, Phasianidae). Data are from 46 accounts of Golden Eagle diet during the breeding season (see Tables 1-3 for details).

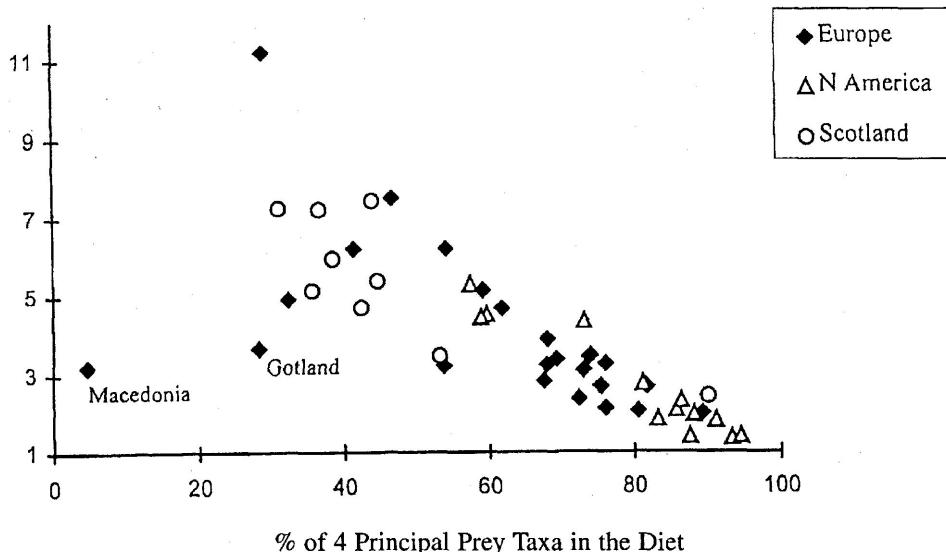


Table 1: Diet of Golden Eagles (% by number) in nine Regions in Scotland during summer

	Region*	1	2	3	4	5	6	7	8	9
Mammals (family)										
Erinaceidae	<i>Hedgehogs</i>			0,7			1,1			
Soricidae	<i>Shrews</i>	0,9			0,7		1,1			
Leporidae	<i>Hares/Rabbits</i>	28,6	34,1	46,9	18,2	13,5	10,7	25,5	42,2	24,8
Muridae	<i>Rats/Mice/Voles</i>	7,1	4,7	0,7	10,9	6,8	7,9	6,4	2,5	5,0
Canidae	<i>Foxes/Dogs</i>		1,2		1,5	2,0	2,8	4,3	0,6	2,8
Mustelidae	<i>Weasels/Badgers</i>	1,8		5,6	2,2	2,0	2,3	2,1	2,5	1,8
Cervidae	<i>Deer</i>	5,4	1,2	8,4	15,3	22,3	19,8	14,9	3,7	14,7
Bovidae	<i>Sheep/Goats</i>	26,8	25,9	23,1	16,8	17,6	18,6	23,4	0,6	15,6
Birds (family)										
Procellariidae	<i>Petrels</i>	17,0	11,8	2,1	8,0					
Phalacrocoracidae	<i>Cormorants</i>					0,6				
Ardeidae	<i>Herons</i>				0,7					
Anatidae	<i>Ducks/Geese</i>			0,7	2,9	2,0	1,7	2,1		2,8
Accipitridae	<i>Hawks/Eagles</i>	0,9								
Falconidae	<i>Falcons</i>					0,7	1,1			
Tetraonidae	<i>Grouse</i>	5,4	8,2	6,3	18,2	25,0	20,3	19,1	47,8	12,8
Phasianidae	<i>Pheasants</i>	1,8			0,4					2,8
Rallidae	<i>Rails</i>			0,7						
Charadriidae	<i>Plovers</i>	1,8		2,1	0,7	1,4	1,1			2,8
Scolopacidae	<i>Sandpipers/Snipe</i>		5,9			0,7				
Laridae	<i>Gulls</i>				0,4		2,3			0,9
Columbidae	<i>Pigeons</i>					0,7				4,6
Strigidae	<i>Owls</i>						1,1			
Alaudidae	<i>Larks</i>				0,4		2,3			
Motacillidae	<i>Pipits</i>	0,9	3,5	2,1	0,7	2,0	0,6	2,1		2,8
Turdidae	<i>Thrushes/Chats</i>					0,7				1,8
Corvidae	<i>Crows</i>	1,8	3,5	0,7	1,1	2,0	4,0			4,6
Reptiles (Order)										
Ophidia	<i>Snakes</i>				0,4	0,7	0,6			
Amphibians										
					0,4					
Sample size		112	85	143	274	148	177	47	161	109
Number of nests		26	23	29	29	38	25	16	28	3
Trophic Diversity		5,14	4,71	3,47	7,21	5,94	7,25	5,38	2,44	7,43

* Regions 1,2 and 3 are Scottish Islands, 4,5,6,7 and 9 west Scotland and 8 east Scotland.

Table 2: Golden Eagle Diet as reported in 24 studies from continental Europe and Asia.

Source		1	2	3	4	5	6	7	8	9	10	11	12
Mammals (family)													
Erinaceidae	Hedgehogs				42,5	28,6	0,3						
Soricidae	Shrews						0,3						
Talpidae	Moles/Desmans						0,3						
Leporidae	Hares/Rabbits	25,8	23,6	20,7	25,6	15	20,9	28,8	10,7	6,8	37,4	1,2	52,3
Hystricidae	Porcupines										33,7		
Sciuridae	Squirrels/Marmots	1	2,6	0,4	1,4	7,5	0,5	5,8	48,4	68,9	4	7,2	3,7
Muridae	Rats/Mice/Voles	2,6	2,7	1,4	0,2	1,5	0,9	0,5	0,7			0,5	0,9
Gliridae	Dormice												
Canidae	Foxes/Dogs	0,9	0,7	1,7	0,2	3	1,3	5,6	2,3	0,7	4	3,6	0,9
Mustelidae	Weasels/Badgers	0,6	0,7	1,8		2,3	1,4	5,8	1,3	1,7	2,5	3,6	10,1
Viverridae	Génet											1,2	
Felidae	Cats				0,1	0,5		0,7	3,2	0,7	0,5	1	
Equidae	Horses												
Suidae	Pigs								0,3	0,5	1		
Cervidae	Deer	9,3			8,2		10,5	0,1	13,5	14,6	2,4	3,5	
Bovidae	Sheep/Goats				0,1	1,1				2,3	5	8,1	3,6
Birds (family)													
Gaviidae	Divers				0,2			0,1					
Ardeidae	Herons					0,2		0,5					
Anatidae	Ducks/Geese	5,9	5,8	3,8	15,4	3	14,4	0,5				1,2	
Pandionidae	Osprey						0,1						
Accipitridae	Hawks/Eagles	0,5	0,4	0,5	0,5	1,5	0,5	2,6			1,2	2	
Falconidae	Falcons				0,1				0,3				
Tetraonidae	Grouse	47,6	55,5	54,3	0,2	18,1	47,8	8,7	13,6	2,4	17,7	13,2	11,9
Phasianidae	Pheasants						1,1	0,8	3,4	1,3	2,4		
Gruidae	Cranes	1,7	5,5	0,7	0,2	6,8	2,4						
Otididae	Bustards												
Haematopodidae	Oystercatchers				0,2								
Burhinidae	Stone Curlews												
Charadriidae	Plovers					0,2		0,5	0,5				
Scolopacidae	Sandpipers/Snipe				0,3	1,9	0,8	3,8	1,1				
Laridae	Gulls					1,7		0,1					
Alcidae	Auk					0,3							
Columbidae	Pigeons				0,1	2,6			7,4		0,2	2	1,2
Cuculidae	Cuckoos						0,1	0,3					
Tytonidae	Barn Owls											2,4	1,8
Strigidae	Owls	0,4	0,4	1,4	0,2	0,8	0,6	2,4					
Picidae	Woodpeckers				0,2		0,1						
Alaudidae	Larks											1,2	
Motacillidae	Pipits							0,1					
Laniidae	Shrikes							0,1					
Turdidae	Thrushes/Chats	1,5	1,3	0,1	0,2		0,3	1,1	0,3	1,9	1	7,2	1,8
Fringillidae	Finches			0,1									
Sturnidae	Starlings											4,8	
Corvidae	Crows	2	1	4,2	3,9		2	7,4	3,6	2,6	9,6	10,8	8,3
Reptiles (Order)										2,4	5,6		
Chelonia	Tortoises												
Squamata	Lizards								0,3			1,2	
Ophidia	Snakes	0,2	0,1		0,2			0,5				2,4	0,9
Amphibians													
Sample size		3766	1796	2792	645	133	749	378	308	424	198	83	109
Number of nests		>50	>50	105	>3	4	>10	>10	>65	17	6	5	7
Trophic Diversity		3,26	2,69	2,87	3,66	6,2	3,38	7,5	3,47	2,06	5,14	6,2	3,23
Source													
1 Sulkava et al. (1984)	7 Danko (in litt.)												
2 Sulkava et al. (1984)	8 Glutz von Blotzheim et al. (1971)												
3 Tjernberg (1981)	9 Huboux (1987)												
4 Hogstrom & Wiss (1992)	10 Huboux (1987)												
5 Zastrov (1946)	11 Austruy & Cugnassee (1981)												
6 Ivanovsky (1990)	12 Mathieu & Choisy (1982)												
	13 Clouet (1981)												
	14 Novelletto & Petretti (1980)												
	15 Magrini et al. (1987)												
	16 Seminaro et al. (1987)												
	17 Fernandez (1987)												
	18 Jordano (1981)												
	19 Delibes et al. (1975)												
	20 Delibes et al. (1975)												
	21 Delibes et al. (1975)												
	22 Grubac (1987)												
	23 Varshavski (1968)												
	24 Yamanoi (1984)												

Table 2: Cont.

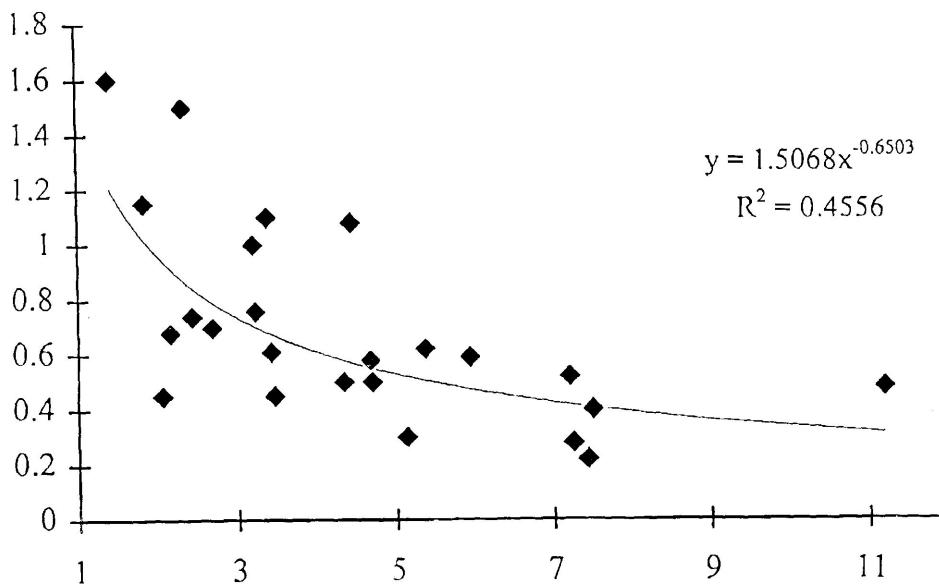
	Source	13	14	15	16	17	18	19	20	21	22	23	24
Mammals (family)													
Erinaceidae	Hedgehogs						1,5	0,4					
Soricidae	Shrews												
Talpidae	Moles/Desmans												
Leporidae	Hares/Rabbits	3,5	48,8	39,6	29,7	67,3	63,1	38,5	48,5	66,5	4,7	10,1	49,5
Hystricidae	Porcupines	0,6											
Sciuridae	Squirrels/Marmots	5,3	4,4	6									
Muridae	Rats/Mice/Voles	7	0,6	10,7				3,1	2,4	0,9		3,5	43,1 11,2 0,2
Gliroidae	Dormice			0,6	0,7	1							
Canidae	Foxes/Dogs	4,4	2,5	2,7	13,5						1,2	5,9	0,5
Mustelidae	Weasels/Badgers	1,8	3,8	6		1		1,6				1,2	0,8
Viverridae	Genet												
Felidae	Cats				1,3							2,4	
Equidae	Horses		0,9									1,2	
Suidae	Pigs		0,9				2,7					2,4	
Cervidae	Deer	14,9										5,9	
Bovidae	Sheep/Goats	4,4	0,6	0,7	14,9	4,8			0,8			8,2	1,6
Birds (family)													
Gaviidae	Divers												
Ardeidae	Herns												
Anatidae	Ducks/Geese												
Pandionidae	Osprey												
Accipitridae	Hawks/Eagles	4,4	1,3					6,2					
Falconidae	Falcons		0,6	1,3		1							
Tetraonidae	Grouse	15,8											
Phasianidae	Pheasants	4,4	20,6	16,1	2,7	8,7	9,2	28,7	24,5	22,8		0,5	17,8
Gruidae	Cranes												
Otididae	Bustards							0,4					
Haematopodidae	Oystercatchers												
Burhinidae	Stone Curlews									1,7			
Charadriidae	Plovers												
Scolopacidae	Sandpipers/Snipe												
Laridae	Gulls												
Alcidae	Aukts												
Columbidae	Pigeons		1,3	1,3			1,9	3,1	2	0,9	1,2		0,6
Cuculidae	Cuckoos												
Tytonidae	Barn Owls								0,4				
Strigidae	Owls		0,6							0,4			
Picidae	Woodpeckers												
Alaudidae	Larks								0,8				
Motacillidae	Pipits								0,4				
Laniidae	Shrikes												
Turdidae	Thrushes/Chats	3,5	1,3	1,3	8,1	2,9	7,7						0,2
Fringillidae	Finches												
Sturnidae	Starlings			0,7									
Corvidae	Crows	7,9	6,3	10,1	2,7	4,8	3,1	9,3	0,9	0,6		1,1	0,3
Reptiles (Order)		2,5											
Chelonia	Tortoises										52,9	31,9	
Squamata	Lizards	8,8											
Ophidida	Snakes	9,7	3,8	1,3	25,7	2,9	1,5	13	12,7	6			27,5
Amphibians		2,6											
Sample size		114	160	149	74	104	65	247	229	167	85	188	967
Number of nests		>10	5	>7	>10	30	6	3	2	3	19	?	?
Trophic Diversity		11,2	3,43	4,69	4,92	2,13	2,38	3,88	3,11	2,01	3,2	3,22	2,83
Location													
1 N Finland		7	Slovakia				13	France (Pyrenees)			19	NW Spain	
2 S Finland		8	Switzerland				14	Italy (Apennines)			20	Spain (Central)	
3 Sweden		9	France (Alps)				15	Italy (Apennines)			21	SW Spain	
4 Sweden (Gotland)		10	France (Alps)				16	Italy (Sicily)			22	Macedonia	

Table 3: Golden Eagle Diet as reported from 13 studies in North America

Source		1	2	3	4	5	6	7	8	9	10	11	12	13
Mammals (family)														
Didelphidae	Opossums											0,4		
Talpidae	Moles/Desmans											0,2		
Leporidae	Hares/Rabbits	32,1	0,4	59,1	0,5	69,8	72,7	72,8	2,6	12,8	85,6	28,8	41,2	65,8
Erethizontidae	Porcupines					0,1					0,1			0,1
Chinchillidae	Chinchillas						0,1							
Sciuridae	Squirrels/Marmots		84,2	27,3	84	12,1	8,3	4	41,8	40,4	4,7	27,8	17,6	19,6
Geomysidae	Pocket Gophers					0,5		0,3		2,1		0,6		0,1
Heteromyidae	Kangaroo Rats						0,2	1,1			0,1			
Muridae	Rats/Mice/voles	1,9	4,8	6,1	0,5	1,1	1	1,1	1,3		0,4	1,4	2,9	0,7
Canidae	Foxes/Dogs								1,6		0,5	0,2	5,9	0,2
Procyonidae	Raccoons										0,4			1,4
Mustelidae	Weasels/Badgers	13,2		1,5	0,5	1,1	0,2				0,2	4	8,8	0,4
Felidae	Cats						0,1					0,8		
Equidae	Horses								0,3					
Cervidae	Deer		3,5		1	2,5	0,1		3,9	6,4	0,1	12,7	2,9	
Antilocapridae	Pronghorns					0,3					0,3			
Bovidae	Sheep/Goats		2,2			0,1			0,3		0,4			6,6
Birds (family)														
Podicipedidae	Grebes										0,1			
Ardeidae	Herons								0,3			0,2		
Anatidae	Ducks/Geese	1,9		1,5			0,4		1,6	2,1	1	0,4		
Accipitridae	Hawks/Eagles		0,2			0,2		0,7	0,3	2,1		0,8		8,8
Falconidae	Falcons					0,1	0,2	0,9	0,6		0,1	0,2		
Tetraonidae	Grouse	49,1	3		10	3,1	0,1	14,5	4,3	0,6		0,6	0,8	
Phasianidae	Pheasants					3,1	10	6,4	14,2	2,1	2,4			
Rallidae	Rails						0,2				0,4			
Scolopacidae	Sandpipers/Snipe						0,1	0,1			0,1			
Laridae	Gulls			1,5					0,9	0,3				
Columbidae	Pigeons					0,1	2,7	0,9	3,5	2,1	0,1			2,9
Cuculidae	Cuckoos											0,4		
Tytonidae	Barn Owls						0,2				0,1	0,2		
Strigidae	Owls					0,9	0,3	0,9	0,6		0,5	1,4	2,9	
Caprimulgidae	Nighthawks						0,1	0,9						
Picidae	Woodpeckers			1,5	0,4				0,6		0,3	0,4		
Alaudidae	Larks							0,9						
Turdidae	Thrushes/Chats						0,1				0,1			
Emberizidae	Buntings	1,7	1,5											
Icteridae	Amer. Blackbirds						0,1	0,9	0,6		0,1	1,6		
Sturnidae	Starlings					0,2								
Corvidae	Crows	1,9			1,5	4,5	1,3	3,1	9,7	10,6	0,2	7,2	2,9	
Reptiles (Order)								4,8						0,6
Ophidia	Snakes					0,4	1,1		1	14,9	1,6	5,6	2,9	
Fish			1,5				0,2		0,3			3,6		
Sample size		53	690	66	200	980	1297	456	311	47	1154	503	34	993
Number of nests		1	?	17	2	38	28	8	74	2	119	17	7	41
Trophic Diversity		2,76	1,4	2,33	1,4	1,97	1,83	1,86	4,35	4,52	1,36	5,3	4,45	2,09

1 Hatler (1974)	8 Knight & Erickson (1978)	Location	7 Idaho
2 Murie (1944)	9 Eakle & Grubb (1986)	1 Alaska	8 Washington
3 Ritchie & Curatolo (1982)	10 Bloom & Hawks (1982)	2 Alaska	9 Oregon
4 Boag (1977)	11 Carnie (1954)	3 Alaska	10 Nevada
5 McGahan (1968)	12 Thompson et al. (1982)	4 Alberta	11 California
6 Kochert (1972)	13 Molhagen et al. (1972)	5 Montana	12 Arizona
7 Collopy (1983)		6 Idaho	13 New Mexico

Figure 2. Relationship between success (fledged young/pair) and trophic diversity for Golden Eagles from 24 study areas in Scotland, North America and continental Europe.



substantial proportion of the diet then the feeding niche is typically narrow (values of $B < 3$). Also, when the feeding niche is narrow eagles tend to breed more successfully. Steenhof and Kochert (1988) working in Idaho found between year differences in trophic diversity amongst Golden Eagles. They showed that niche breadth expanded in years when the preferred prey of Black-tailed Jackrabbits *Lepus californicus* was scarce. They were also able to test whether this was due to most pairs in the population having a more varied diet, or to certain individuals specialising on different prey species. They concluded that increased trophic diversity in the population was a result of most pairs having a more diverse diet, rather than specialisation on different prey by certain pairs only. Work in Idaho has also shown that Golden Eagle breeding success is reduced when jackrabbit numbers are low (Kochert, 1980).

In Scotland grouse and hares are much more plentiful in the east Highlands than in the west (Watson *et al.* 1992). Such differences between the oceanic west and more continental east are linked to the abundance of heather *Calluna vulgaris* which is a staple food of Red Grouse and Mountain Hares. Historically numbers of grouse and hares were much higher throughout much of the Highlands. Declines have been attributed to the past 150 years of excessive sheep grazing, further exacerbated recently by large numbers of Red Deer *Cervus elaphus* (McVean & Lockie, 1969). Whilst there are no

comparable data on Golden Eagle breeding success from a time when grouse and hares were more plentiful, it would seem likely that breeding success was then much higher, at least in the west Highlands. Nowadays eagles in that region must take a broad spectrum of prey, and to do so they will necessarily require to use a range of hunting strategies. The need for an eagle to constantly modify its hunting behaviour in order to catch a diverse range of prey may result in reduced hunting efficiency. This may be one reason why eagles with a broader feeding niche tend to breed less successfully than those with a narrow diet. Another, and perhaps more important factor, which probably contributes to reduced breeding performance is the comparative lack of sufficient prey in the eagle's optimum size range (animals around 1-3 kg in weight). This has resulted in an over-dependence on large prey (>4 kg) such as young ungulates, and consequent inefficiencies when such items must be carried to nest sites. So, at least in the west of Scotland, the eagle's broad spectrum diet is consistent with the hypothesis that conditions there are currently less than optimal.

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