

Diet of the Golden Eagle *Aquila chrysaetos* in two areas on the southern slopes of the Catalan Pyrenees

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We provide quantitative information regarding the diet of the Golden Eagle *Aquila chrysaetos* during the breeding season in two different areas on the southern slopes of the Catalan Pyrenees (NE Spain). Food remains and pellets were collected at nests after chicks had fledged in two study sites, Pallars and Cerdanya, on central and eastern Pyrenees respectively. Six territories were sampled in Pallars in 2001–2005 and four in Cerdanya in 2008, totalling 11 and four territory/year diet samples respectively, from which 205 prey items were identified. In Cerdanya, 44% of prey items were Hares, Rabbits or Marmots, 18% ungulates, 11% corvids and 9% small passerines, followed by 4% small mammals, 4% gamebirds, 2% carnivores and 2% pigeons. In Pallars, only 21% of prey items were Hares, Rabbits or Marmots, 15% were ungulates, 9% corvids and 4% small passerines. However, the eagles in Pallars consumed larger amounts of other prey types: 17% small mammals, 11% carnivores, 10% gamebirds, 4% pigeons and 4% birds of prey. The Ptarmigan *Lagopus muta*, a target species of conservation concern, accounted for 2.4% of all prey. Our results suggest that, in areas where eagles prey, above all, on Hares and Marmots, their dietary diversity was lower, whereas in areas where these prey types were less frequently captured, the prey-size distribution was more left-skewed and dietary diversity increased. The capture of small and medium sized predators was more frequent in the area where the intake of Hares and Marmots was lower. The adjustment in the consumption of meso-predators as a function of the availability of the main prey types may have effects on the regulation of the whole community.

Key words: Golden Eagle, *Aquila chrysaetos*, predation, dietary habits, birds of prey, Catalonia.

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The Golden Eagle *Aquila chrysaetos* is a large bird of prey that is widely distributed throughout North America and Eurasia (Cramp & Simmons 1980, del Hoyo *et al.* 1994). It is well adapted to many types of environments, from high mountains to lowlands, and from forest to steppes.

Outside the Pyrenees, its diet has been studied in detail in many parts of the world (Delibes *et al.* 1975, Olendorf 1976, Tjernberg 1981, Sulkava *et al.* 1984, Huboux 1987, Höglstrom & Wiss 1992, Moleón *et al.* 2002, Takeuchi *et al.* 2006, Watson 2010) and it is clear that this eagle is

a very eclectic predator, feeding mainly on any available medium-sized (250–4000 g) mammal or bird, but also on reptiles and carrion (del Hoyo *et al.* 1994, Watson 2010). Its diet may also include livestock, game and gamebirds, as well as a wide range of medium-sized mammal and avian predators (Watson 2010). Hence, the Golden Eagle plays a significant role in the regulation of prey communities (i.e. Valkama *et al.* 2005, Lyly *et al.* 2016) and meso-predator assemblages (Fielding *et al.* 2003, Sergio & Hiraldo 2008, Lyly *et al.* 2015) but can also be the origin of conflicts with farmers (Norberg *et al.* 2006, Watson 2010) and hunters (Newton *et al.* 2021).

The Golden Eagle is currently the largest avian predator in the Pyrenees, a mountain range in southern Europe of great biogeographical and conservation interest (Martínez Rica & Montserrat 1990, Schmitt 2009). Given the significant role that it may have in the organization of vertebrate communities, a number of studies have analysed the diet and trophic ecology of this raptor in the region (Clouet & Goar 1980, Clouet 1981, Fernandez & Purroy 1990, Fernández 1991, Goar & Clouet 2014, Clouet *et al.* 2017). However, previous research has focussed on areas containing no genuine alpine communities and species, such as the Ptarmigan *Lagopus muta*, Marmot *Marmota marmota* and Pyrenean Chamois *Rupicapra pyrenaica*. Our research aimed to fill this gap by providing additional quantitative information on the diet of the Golden Eagles in the Pyrenees, which will contribute to the understanding of the role of this species in the structuring and regulation of vertebrate communities in this southern European mountain range.

Material and methods

Food remains were collected in two different study areas in the Catalan Pyrenees (NE Spain) (Figure 1), which at that time held a Golden Eagle population of 70–76 breeding pairs (Beneyto *et al.* 2004). The Pallars study area lies within the counties of El Pallars Jussà, El Pallars Sobirà and L'Alta Ribagorça, to the south of the Aigüestortes i Estany de Sant Maurici National Park, and is representative of the conditions found on the south-facing slopes of the central Pyrenees. It lies in the core area

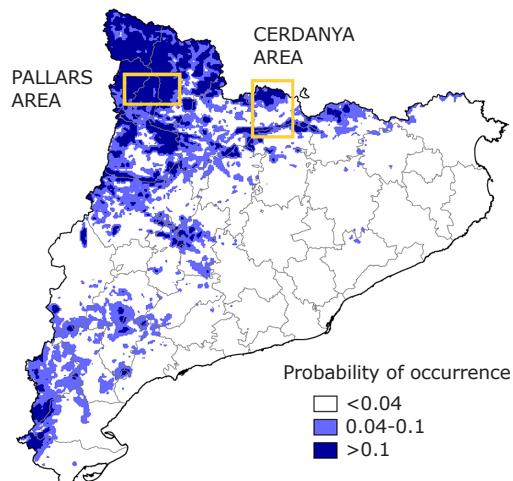


Figure 1. Golden Eagle *Aquila chrysaetos* distribution in Catalonia during the breeding season, according to Estrada *et al.* (2004), with indication of the location of both study areas. White areas indicate very low probability of occurrence and darker areas correspond to higher probability of occurrence.

Distribució de l'àguila daurada *Aquila chrysaetos* a Catalunya durant el període reproductor segons Estrada *et al.* (2004), amb indicació de la ubicació d'ambdues àrees d'estudi. Les zones blanques indiquen una probabilitat d'aparició molt baixa i les més fosques corresponen a una probabilitat d'aparició més alta.

of this eagle's range in the Pyrenees (del Moral 2009) (Figure 1) and possesses one of the highest Golden Eagle densities ($78 \text{ km}^2/\text{pair}$) in Catalonia (Beneyto *et al.* 2004, Garcia & Parellada 2009). The Cerdanya study area lies within the county of La Cerdanya, in the eastern Pyrenees, on the edge of the Golden Eagle's distribution (del Moral 2009) and has a lower eagle density (Figure 1; see Garcia & Parellada 2009).

Within 10 days of chick fledging, experienced climbers collected prey remains (i.e. bones, feathers, skin, hair, etc.) and pellets from the empty nests. Six territories were sampled in the Pallars from 2001-2005 and four in the Cerdanya in 2008, giving a total of 11 and four territory/year

Table 1. Number (N) and relative frequency (%) of prey items in the diet of Golden Eagles in Pallars and Cerdanya study areas. The Simpson Diversity Index (1/D) of the diet in each area is shown in the final row. Nombre (N) i freqüència relativa (%) de preses a la dieta de l'àguila daurada a les àrees d'estudi Pallars i Cerdanya. L'índex de diversitat de Simpson (1/D) de la dieta en cada una de les àrees es mostra al darrer rengle.

	N PALLARS	N CERDANYA	N TOTAL	% PALLARS	% CERDANYA	% TOTAL
<i>Marmota marmota</i>	10	5	15	6.25	11.11	7.32
<i>Lepus europaeus</i>	21	11	32	13.13	24.44	15.61
<i>Oryctolagus cuniculus</i>	3	4	7	1.88	8.89	3.41
Total large rodents and lagomorphs <i>Total grans rosegadors i lagomorfs</i>				21.25%	44.44%	26.34%
<i>Talpa europaea</i>	11	0	11	6.88	0.00	5.37
<i>Neomys fodiens</i>	0	1	1	0.00	2.22	0.49
<i>Elyomis quercinus</i>	1	0	1	0.63	0.00	0.49
<i>Apodemus sylvaticus</i>	2	0	2	1.25	0.00	0.98
<i>Microtus</i> sp.	1	0	1	0.63	0.00	0.49
<i>Microtus nivalis</i>	1	0	1	0.63	0.00	0.49
<i>Microtus agrestis</i>	0	1	1	0.00	2.22	0.49
<i>Arvicola terrestris</i>	11	0	11	6.88	0.00	5.37
Total small mammals <i>Total petits mamífers</i>				16.88%	4.44%	14.15%
<i>Ovis aries</i>	0	1	1	0.00	2.22	0.49
<i>Capreolus capreolus</i>	0	2	2	0.00	4.44	0.98
<i>Rupicapra rupicapra</i>	16	2	18	10.00	4.44	8.78
<i>Sus scrofa</i>	5	3	8	3.13	6.67	3.90
Undetermined ungulates <i>Ungulat indeterminat</i>	3	0	3	1.88	0.00	1.46
Total ungulates <i>Total ungulats</i>				15.00%	17.78%	15.61%
<i>Martes foina</i>	5	0	5	3.13	0.00	2.44
<i>Mustela vison</i>	1	0	1	0.63	0.00	0.49
<i>Mustela erminea</i>	1	0	1	0.63	0.00	0.49
<i>Meles meles</i>	4	0	4	2.50	0.00	1.95
<i>Genetta genetta</i>	1	0	1	0.63	0.00	0.49
<i>Vulpes vulpes</i>	5	1	6	3.13	2.22	2.93
<i>Canis familiaris</i>	1	0	1	0.63	0.00	0.49
Total carnivores <i>Total carnívors</i>				11.25%	2.22%	9.27%
TOTAL MAMMALS				64.38%	68.89%	65.37%
TOTAL MAMÍFERS						
<i>Lagopus muta</i>	4	1	5	2.50	2.22	2.44
<i>Alectoris rufa</i>	6	1	7	3.75	2.22	3.41
<i>Perdix perdix</i>	6	0	6	3.75	0.00	2.93
Total gamebirds						
Total Galliformes				10.00%	4.44%	8.78%
<i>Columba livia</i>	1	0	1	0.63	0.00	0.49
<i>Columba palumbus</i>	0	2	2	0.00	4.44	0.98
<i>Columba</i> sp.	3	0	3	1.88	0.00	1.46
Total pigeons <i>Total coloms</i>				2.50%	4.44%	2.93%
<i>Garrulus glandarius</i>	9	2	11	5.63	4.44	5.37
<i>Pyrrhocorax</i> sp.	5	1	6	3.13	2.22	2.93
<i>Corvus corax</i>	1	0	1	0.63	0.00	0.49
<i>Corvus</i> sp.	0	1	1	0.00	2.22	0.49
<i>Corvid</i> sp.	0	1	1	0.00	2.22	0.49
Total corvids <i>Total còrvids</i>				9.38%	11.11%	9.76%
<i>Falco tinnunculus</i>	5	0	5	3.13	0.00	2.44
<i>Accipiter gentilis</i>	1	0	1	0.63	0.00	0.49
Total birds of prey				3.75%	0.00%	2.93%
Total ocells rapinyaires						
<i>Turdus viscivorus</i>	7	0	7	4.38	0.00	3.41
<i>Turdus torquatus</i>	0	1	1	0.00	2.22	0.49
<i>Turdus viscivorus/philomelos</i>	0	1	1	0.00	2.22	0.49
<i>Emberiza cia</i>	0	1	1	0.00	2.22	0.49
<i>Parus ater</i>	0	1	1	0.00	2.22	0.49
Total small passerines				4.38%	8.89%	5.37%
Total petits passeriformes						
TOTAL BIRDS TOTAL OCELLS	48	13	61	30.00%	28.89%	29.76%
<i>Timon lepidus</i>	2	0	2	1.25	0.00	0.98
<i>Podarcis muralis</i>	1	0	1	0.63	0.00	0.49
<i>Natrix natrix</i>	0	1	1	0.00	2.22	0.49
Undetermined snakes <i>Serp indeterminada</i>	5	0	5	3.13	0.00	2.44
Undetermined fish <i>Peix indeterminat</i>	1	0	1	0.63	0.00	0.49
TOTAL REPTILES AND FISH				5.63%	2.22%	4.88%
TOTAL RÉPTILS I PEIXOS						
Total Total	160	45	205			
1/D				7.44	4.18	

Table 2. Comparison of diet composition between both study areas. Bold figures indicate significant differences between observed and expected frequencies according to the standardised corrected residuals > 1.96 .
Comparació entre la composició de la dieta entre les dues àrees d'estudi. Les xifres en negreta indiquen diferències significatives entre les freqüències observades i esperades segons els residus corregits estandarditzats > 1.96 .

	PALLARS		CERDANYA	
	Nº of prey N de preses	%	Nº of prey N de preses	%
Hare, Rabbit and Marmot <i>Llebre, conill i marmota</i>	34	21.25	20	44.44
Small mammals <i>Petits mamífers</i>	27	16.88	2	4.44
Ungulates <i>Ungulats</i>	24	15.00	8	17.78
Other prey <i>Altres preses</i>	75	46.87	15	33.33

diet samples respectively. Remains and pellets were frozen separately before hairs, feathers and bones were analysed and identified using specialised guides (Pales & Lambert 1971, Debrot 1982) and our own reference collections. As the independent study of prey remains or pellets offers a biased picture of diet composition (Martí *et al.* 2007), the total number of prey items was estimated as the minimum number of individuals represented in the combined sample of remains and pellets found in each nest and year (Seguin *et al.* 1998), taking into account whenever possible the species, size and sex differences of the samples. The composition of prey-type and -weight distributions in the two areas was compared using the Fisher Exact Test. The standardized corrected residuals with absolute values > 1.96 were employed to indicate significant observed-frequency departures from expected values. Dietary diversity in each area was computed using the inverse (1/D) of the Simpson Index D:

$$D = \frac{\sum n \cdot (n-1)}{N \cdot (N-1)}$$

where N is the total number of prey items and n is the number in each of the following 10 prey categories: Large rodents and lagomorphs, Small mammals, Ungulates, Carnivores, Gamebirds, Pigeons, Corvids, Birds of prey, Small passerines, Reptiles and Fish.

Results

The samples contained 251 different prey items, in a range of 1–26 prey items per nest but only

the 205 prey items identified to order level were considered for further analysis. The diet of the Golden Eagle in the study areas included mammals (65.4%), birds (29.8%) and other prey (4.9%), such as reptiles and fish (Table 1). The most important prey types were medium-sized mammals, such as Hares *Lepus europaeus* (15.6%) and Marmots (7.3%), followed by ungulates, mainly the Pyrenean Chamois (8.8%). Small mammals (rodents, shrews and moles) were also important, including Northern Water Vole *Arvicola terrestris* (5.4%) and Northern Mole *Talpa europaea* (5.4%). The eagles also ate a remarkable number of carnivores, including Red Fox *Vulpes vulpes* (3.1%), Pine Marten *Martes martes* (3.1%) and Badger *Meles meles* (2.5%). Among birds, corvids were dominant (9.8%), closely followed by gamebirds (8.8%), including Ptarmigan (2.4%). Their diet included small passerines (5.4%) and pigeons (2.9%), as well as other birds of prey (2.9%). They also captured snakes (2.9%), lizards (1.5%) and fish (0.5%).

In both areas, large rodents (Marmots) and lagomorphs (Rabbits and Hares) were the commonest prey. Considering the four prey categories with expected frequencies > 5 (Large rodents and lagomorphs; Small mammals; Ungulates; Other prey, Table 2), the differences between the two regions were significant (Fisher exact test = 12.275, P = 0.006). The eagles in Cerdanya consumed higher amounts of large rodents and lagomorphs and fewer small mammals than expected, while eagles in Pallars ate fewer large rodents and lagomorphs but more small mammals. The eagles' diet was less diverse

in Cerdanya than in Pallars, where a greater proportion of small mammals, carnivores, game-birds, birds of prey and reptiles compensated for fewer Hares, Rabbits and Marmots. Although the overall proportion of ungulates was similar in both areas, there was a higher proportion of Chamois in Pallars than in Cerdanya. This was also reflected in the size of the prey items consumed in the two areas, which was larger in Cerdanya (most captures 633–2714 g) than in Pallars (most captures 148–632 g) (Fisher Exact test = 11.618, P = 0.034; Figure 2). According to the typified corrected residuals, only the proportion category 35–147 g was significantly different between the two study areas.

Discussion

Large predators such as the Golden Eagle are able to exert top-bottom effects on biological communities (Watson 2010). For this reason, detailed quantitative knowledge of the diet of such predators is key to understanding the interactions between predator and prey populations and potential cascading effects. Our results are consistent with previous findings indicating that, despite being a generalist and opportunistic predator, Golden Eagles target prey – particularly mammals – in the weight range 500–3000 g, as reported in other Eurasian or American areas (see review in Watson 2010).

The European Hare was the most important single prey species in both of our study sites, particularly in Cerdanya, where they accounted for up to a quarter of the captured prey items. Lagomorphs and Marmots accounted for almost half of the diet in the Cerdanya and a fifth in Pallars, thereby confirming that, when available, medium-sized mammals are probably the optimal prey type for Golden Eagles. The differences observed between sites were probably associated with differences in the abundances of these and other alternative sorts of prey. In Cerdanya, the eagles' diet was centred on this apparently optimal prey species, whereas in Pallars there was a preponderance of smaller species, including many sorts of small mammals and birds, which thus entailed greater dietary diversity. A similar inverse relationship between dietary diversity and prey weights was observed by Clouet *et al.* (2017) when comparing the diet of golden eagles in the Corbières and the Basque country, at opposite ends of the Pyrenees.

Ungulates were predated upon at similar rates in the two areas, although it was impossible to determine whether or not large ungulates were killed by eagles or eaten as carrion. Indeed, scavenging and kleptoparasitism are regularly practiced by birds of prey (including eagles), especially by inexperienced individuals and/or in low quality habitats (Sánchez-Zapata *et al.* 2010, Margalida *et al.* 2017). Nonetheless, in our study area the percentage of ungulates in the

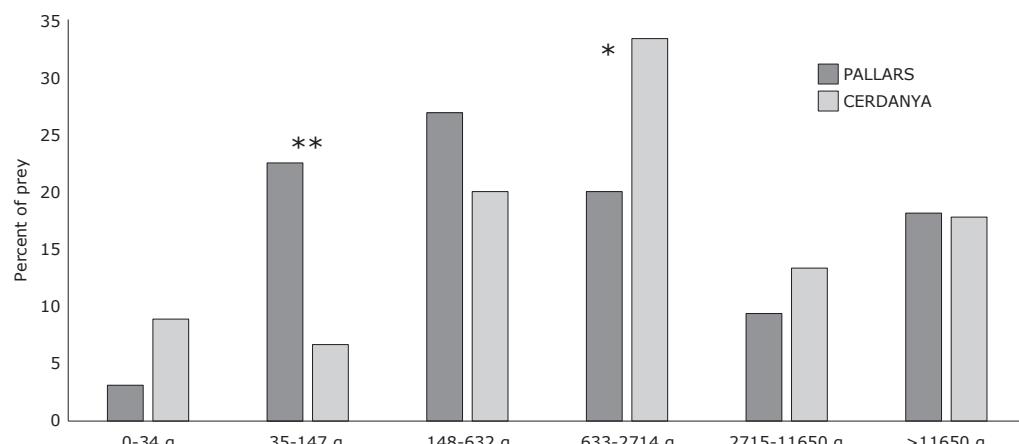


Figure 2. Distribution of prey items according to weight in Pallars and Cerdanya. Categories where the differences in frequencies between areas are significant (**: P<0.05) or marginally significant (*) are indicated. *Distribució de les preses segons el seu pes a Pallars i Cerdanya. S'indiquen les categories en què la diferència de freqüència entre àrees és estadísticament significativa (**: P<0.05) o marginalment significativa (*).*

diet was comparable to the figures reported in other parts of the world (Watson 2010) where, in general, ungulates are never dominant in the diet of Golden Eagles. The smaller proportion of Pyrenean Chamois in the eagles' diet in Cerdanya than in Pallars may be the result of the lower abundance of this mammals in the former region as a consequence of the greater virulence of the pestivirus outbreak in 2001 (Marco et al. 2009).

The Marmot was introduced into the Pyrenees in 1948–1988 to, amongst other reasons, provide prey for Golden Eagles and ease the predation pressure on the Pyrenean Chamois (López et al. 2009, 2010). Our results suggest that, although eagles do consume Marmots in reasonable amounts, Hares are still their preferred prey, as seems to occur in many other areas of the world where both these prey species are present and consumed (Watson 2010). Although Marmots are locally abundant and visible, they are patchily distributed and are only available during the warm months of the year. Additionally, their social behaviour and alarm calls probably make them more difficult to capture than either Rabbits or Hares.

The different proportions of Marmots in the diet of eagles in both sites may simply reflect differences in the abundances of this and other sorts of prey, although the lack of historical information on Marmot abundance and eagle diet hinders a more detailed understanding of this relationship.

Birds of different types and sizes were frequently taken in both areas, a finding that is consistent with the results reported by Clouet (1981) and Clouet et al. (2017). Corvids were consumed in similar proportions in both areas and seem to be relatively important, while pigeons only represented a relatively small part of the eagles' diets in both sites. Small passerines were relatively important in Cerdanya, while in Pallars gamebirds were captured more often and, interestingly, birds of prey appeared in the eagles' diet. Although grouse species are important prey for the Golden Eagles in many European areas (Valkama et al. 2005, Watson 2010), the proportion of Ptarmigan in the diet in both our study sites was low and consistent with values reported from other Pyrenean areas (Clouet 1981), which may reflect the relatively low availability of Ptarmigans in these mountains. Although numerically not very significant, the

potential negative effect of eagle predation on this grouse species of conservation concern is worth bearing in mind given that the Ptarmigan is rare and declining at both sites as a result of habitat alteration and climate change (Parellada et al. 2004).

Although not as frequently as in other areas of the Pyrenees (Clouet et al. 2017), we found that eagles frequently captured medium-sized carnivores and birds of prey, as in many other parts of the world (Fernandez 1991, Ellis et al. 1999). Our results indicate that this type of prey was more frequently taken in Pallars than in Cerdanya, suggesting that the capture of mammalian and avian meso-predators increased when the consumption of the optimal prey types (i.e. Rabbits, Hares and Marmots) declined. A similar trend was observed by Clouet et al. (2017) and agrees with the expectations of the rules governing intraguild predation (Tella & Mañosa 1993, Sergio & Hiraldo 2008) and may have implications for the regulation of prey populations situated lower down in the trophic web.

To summarize, our results indicate the importance of Hares and Marmots in the diet of the Golden Eagle on south-facing Pyrenean slopes. In agreement with the Optimal Foraging Theory (MacArthur & Pianka 1966, Schoener 1971, Pyke et al. 1977, Stephens & Krebs 1986), our findings suggest that in the areas where eagles concentrate their predation on this type of prey, their diet was less diverse. Conversely, in the areas where they consumed fewer Hares and Marmots, eagles captured larger numbers of other prey (Steenhof & Kochert 1988, Miller et al. 2006, Reif et al. 2009), including small mammals, gamebirds, carnivores and birds of prey, which entailed greater dietary diversity and a more left-skewed prey size distribution.

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Resum

Dieta de l'àguila daurada *Aquila chrysaetos* a dues zones del vessant sud del Pirineu català

Proporcionem informació quantitativa sobre la dieta de l'àguila daurada durant l'època de reproducció al vessant sud del Pirineu català. Vam recollir restes de preses i egagròpiles als nius després de l'envol dels polls a dues zones d'estudi diferents, Pallars i Cerdanya, situades als Pirineus centrals i als Pirineus orientals respectivament. Vam mostrejar sis territoris a Pallars entre 2001–2005 i quatre a Cerdanya el 2008, obtenint un total de 11 i quatre mostres de dieta per territori·any, respectivament, en les quals vam identificar 205 preses. A Cerdanya, el 44% de les preses foren llebres, conills i marmotes, 18% ungulats, 11% còrvids i 9% petits passeriformes, seguits d'un 4% de petits mamífers, 4% de gal·liformes, 2% de carnívors i 2% de coloms. A Pallars, només el 21% de les preses foren llebres, conills i marmotes, 15% ungulats, 9% còrvids i només el 4% petits passeriformes, però les àguiles van consumir comparativament quantitats més grans d'altres preses: 17% de petits mamífers, 11% de carnívors, 10% de gal·liformes, 4% de coloms i també 4% d'ocells rapinyaires. Globalment, la perdix nival *Lagopus muta*, una espècie de preocupació per a la conservació, va representar el 2.4% de les preses. Els nostres resultats suggereixen que, a les zones on les àguiles van concentrar la seva depredació sobre llebres i marmotes, la diversitat tròfica va ser menor, mentre que a les zones on es capturaren menys la distribució de mida de les preses es va desplaçar cap a valors més baixos i la diversitat tròfica es va incrementar. La captura de petits i mitjans depredadors va ser més freqüent a la zona on el consum de les preses suposadament òptimes va ser menor. Aquest ajustament en el consum de mesodepredadors en funció de la disponibilitat de les preses principals podria tenir efectes sobre la regulació del conjunt de la comunitat.

Resumen

Dieta del águila real *Aquila chrysaetos* en dos zonas de la vertiente sur del Pirineo catalán

Presentamos nueva información cuantitativa sobre la dieta del águila real durante la época de cría en la vertiente sur del Pirineo catalán. Recolectamos restos de presas y egagrópiles en nidos después del vuelo de

los pollos, en dos zonas de estudio, Pallars y Cerdanya, situadas en el Pirineo central y Pirineo oriental respectivamente. Tomamos muestras de seis territorios en Pallars entre 2001–2005 y cuatro en Cerdanya en 2008, obteniendo un total de 11 y cuatro muestras de dieta por territorio·año, respectivamente, en las cuales identificamos 205 presas. En Cerdanya, el 44% de las presas fueron liebres, conejos y marmotas, 18% ungulados, 11% còrvidos y 9% pequeños paseriformes, seguidos de un 4% de pequeños mamíferos, un 4% de galliformes, 2% de carnívoros y 2% de palomas. En Pallars, solo el 21% de las presas fueron liebres, conejos y marmotas, 15% ungulados, 9% còrvidos y solo un 4% pequeños paseriformes, pero las águilas consumieron comparativamente mayores cantidades de otras presas: 17% de pequeños mamíferos, 11% de carnívoros, 10% de galliformes, 4% de palomas y también 4% de rapaces. Globalmente, la perdiz nival *Lagopus muta*, una especie de preocupación para la conservación, representó el 2.4% de las presas. Nuestros resultados sugieren que, en áreas donde las águilas concentraron su depredación en liebres y marmotas, la diversidad de la dieta fue menor, mientras que en áreas donde estas presas fueron capturadas con menor frecuencia la distribución del tamaño de las presas se desplazó hacia valores más reducidos y la diversidad trófica se incrementó. La captura de pequeños y medianos depredadores fue más frecuente en la zona donde el consumo de las presas supuestamente óptimas fue menor. Este ajuste en el consumo de mesodepredadores en función de la disponibilidad de presas principales podría tener efectos sobre la regulación del conjunto de la comunidad.

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