Biases in diet sampling methods in the Spanish Imperial Eagle *Aquila adalberti*

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This study quantifies for the first time the biases associated with different methods (direct observations, pellets, remains, and pellets plus remains referred to as pooled data) used to assess the diet of the Spanish Imperial Eagle *Aquila adalberti*. With respect to prey items delivered to the nest as a surrogate of the most objective method to assess the diet, pellets, remains and pooled data overestimated birds and underestimated mammals. With regards to the size of the prey, prey remains, pellets and pooled data underestimate larger prey (>601 g) but overestimated smaller and medium size preys (<300 g and 301–600 g). Concerning dietary breadth, prey remains provided the widest trophic spectrum. Our results suggest that the three methods used to quantify the diet in Spanish Imperial Eagles are significantly different and that the pooled data (pellets plus prey remains) is not a reliable alternative method for direct observations to reduce this bias. Biases in the diet can differ considerably among prey categories, and based on our data it is not possible to generalise about the most appropriate method for estimating raptor diets. Thus, the reported biases should be seriously considered in management and conservation strategies for threatened species based on indirect studies on raptor diet.

1. Introduction

Biases associated with different methods of assessing raptor diets have been analysed for several species (e.g., Collopy 1983, Simmons *et al.* 1991, Mersmann *et al.* 1992, Real 1996, Redpath *et al.* 2001). Of the different methods used, direct observation provides the most complete and accurate estimate, although this method requires a great deal of time (Marti 1987). For this reason, most studies of raptor diets are still based on indirect methods such as the analysis of prey remains and pellets.

The biases inherent in the two last-mentioned methods (prey remains and pellets) have been dealt with in diurnal (e.g., Simmons *et al.* 1991, Mañosa 1994, Tella & Oro 1995, Seguin *et al.* 1998, Redpath *et al.* 2001) and nocturnal (Marchesi *et al.* 2002) raptors. A general view is that prey remains overestimate large and conspicuous prey, while pellets tend to overestimate the occurrence of medium to small prey, such as small mam-

mals and passerine birds. Different solutions have been proposed to minimise these biases. For example, Simmons et al. (1991) suggested that results from pellets and prey remains can be combined to minimise the bias for African Marsh Harrier Circus ranivorus. Real (1996), on the other hand, suggested that the most efficient method for monitoring the diet of Bonelli's Eagle Hieraaetus fasciatus is a pellet analysis. However, Redpath et al. (2001) suggested that for Hen Harrier Circus cvaneus, combined data on pellet and prey remains did not eliminate biases and that pellets are useful for estimating prey diversity but direct observations would be necessary for quantifying the biases inherent in diet estimates. This range of opinion regarding conclusions, suggest that, in raptors, generalisations about the most appropriate method for diet estimates may not be drawn, and that the biases should be assessed at a species level (Redpath et al. 2001, Margalida et al. 2007).

The Spanish Imperial Eagle *Aquila adalberti* is a vulnerable species (BirdLife International 2005), with its population numbering around 200 pairs (González *et al.* 2008). The diet of this species has been analysed by studying pellets and prey remains (Delibes 1978, González 1991), but potential biases in the determination of its diet have not previously been evaluated.

We investigated potential biases that the study of the diet of Spanish Imperial Eagle may be subjected to during the breeding season using a range of dietary assessment methods. We used direct observations, prey remains and pellets to compare prey frequencies, prey biomass and prey diversity. In addition, we tested whether the pooling of pellet and prey remains (as proposed by several studies of other raptor species) could reduce or eliminate these biases.

2. Material and methods

The study was carried out in Extremadura (Cáceres and Badajoz provinces), Spain. In this region, a supplementary feeding programme has been established as a conservation tool to increase the breeding success of Spanish Imperial Eagle (González *et al.* 2006). In this programme, eagle pairs were provided with domestic rabbits to supplement the scarcity of this prey in low-quality territories. For these pairs, the remains and pellets present in the nest were collected after the breeding season. Although the diet may be slightly biased, with the main prey of the eagle (rabbit) being overestimated, the proportion of domestic rabbits in the diet of birds from 18 territories that received supplementary feeding was similar to the proportion of wild rabbit in three nests that did not receive supplementary feeding (88% vs. 86%; González *et al.* 2006). Thus, it is possible to compare diet-assessment methods (prey delivered, prey remains and pellets) to determine which prey items are overestimated in relation to those delivered to the nest.

Diet samples were collected by visually observing prey items being delivered to the nest and by collecting pellets and remains from the nests and under nesting trees after the breeding season. i.e., August-September (González 1991, Margalida et al. 2007a). Prey items delivered to the nest were observed from hides at a distance of <200 m to the nest. The observations and collections were carried out between 1998 and 2001 for 14 pairs of Spanish Imperial Eagle (34 breeding attempts). The observations covered the chick-rearing period (average 77 days; Margalida et al. 2007a, b) so as to avoid temporal biases caused by seasonal variation in the diet. Of a total of 4,669 prey items delivered to the nest, 4,487 were identified and used in this study (average 323.1 ± 156.1 SD identified prey items delivered per pair; n = 14). In addition, 744 pellets were collected. Of these, a total of 1,044 prey items were obtained, of which 997 were identified (average $72.9 \pm 30.9 \pm SD$ identified prey items per pair; n = 14). Finally, 415 remains were collected from the nests (average 41.7 $\pm 34.6 \pm$ SD identified prey items per pair; n = 10). For some pairs we obtained samples from different years to increase the sample size and to minimise the impact of unequal sampling among territories. For each territory in which samples were obtained from multiple years (n = 10), we tested the interannual differences comparing the occurrence of the most important prey categories, i.e., Leporidae and Columbidae. Because no significant differences were found between years/territory (chisquare P > 0.05 for all of the pairs considered), data were pooled. Thus, each territory (not breeding attempt) was considered a sampling unit to avoid pseudoreplication (Katzner et al. 2006).





Prey remains and pellets were identified using the authors' reference collection of bones and feathers. Prey mass was estimated using the literature (Cramp & Simmons 1980, González 1991, Mañosa 1994) and the authors' own data from the study area. Prey mass was categorised as: <300 g (small prey items); 301–600 g (medium-sized prey items) and >601 g (large prey items). To avoid the impact of occasional very large items on the mean prey mass, no items were assigned a mass of >3,000 g (i.e., *Ciconia ciconia* and *Vulpes vulpes*).

The diet was determined separately from identified prey items delivered to the nests, in pellets and remains for each territory. Pellets and prey remains were also pooled by considering the minimum number of prey items identified in each unit sample. Prey items were grouped into family categories.

The dietary specialisation for each method was calculated using Levins' index of diet breadth by including the 34 prey groups (families) that could be accurately identified (Levins 1968, Krebs 1989). The index was calculated for each territory as follows:

$$\mathbf{B} = 1 / \sum_{i=1}^{n} p_i^2 \tag{1}$$

where p_i is the proportion of prey in different categories. To compare diet breadth, we calculated the standardised food niche breadth for samples with different numbers of prey categories following Colwell and Futuyama (1971):

$$\mathbf{B}_{\mathrm{sta}} = (\mathbf{B}_{\mathrm{obs}} - \mathbf{B}_{\mathrm{min}}) / (\mathbf{B}_{\mathrm{max}} - \mathbf{B}_{\mathrm{min}})$$
(2)

where B_{min} is the minimum niche breadth possible (n = 1), $B_{obs} =$ number of prey types observed, and $B_{max} = n$. This index ranges from 0 to 1.

Comparisons of prey taxa or prey mass among the three methods of diet assessment were performed by means of chi-square statistics on contingency tables, applying the Bonferroni correction for multiple probabilities (Zar 1996). The mean number of species identified per detected family was compared among methods using the Kruskal-Wallis test.

3. Results

3.1. Comparison of prey delivered, pellets and prey remains

Of the 4,487 prey items identified, 4,205 corresponded to mammals (93.7%), 262 to birds (5.8%) and 20 to reptiles and amphibians (0.4%). Of the 997 remains identified in the pellets, 664 corresponded to mammals (66.6%), 328 to birds (32.9%) and five to reptiles (0.5%). Of the 415 remains identified, 124 (29.9%) corresponded to mammals, 285 to birds (68.7%) and six (1.4%) to reptiles. Significant differences were found between prey delivered to the nest and the pellet data ($\chi^2_2 = 622.79, P < 0.0001$) and the remains data ($\chi^2_2 = 311.97, P < 0.0001$). Pellets and remains thus appeared to overestimate birds and underestimate mammals.

The analysis for the frequency of prey by weight categories also indicated significant differ-

Table 1. Number of prey items (Np) and species (Ns) identified using different sampling methods to assess the diet of the Spanish Imperial Eagle (n = 14 pairs).

Taxon	Delivered			Pellets			Remains			Pooled		
	Np	%	Ns	Np	%	Ns	Np	%	Ns	Np	%	Ns
Aves												
Turdidae	13	0.29	2	6	0.60	4	14	3.37	2	15	1.29	3
Corvidae	37	0.82	4	64	6.42	5	78	18.80	5	88	7.58	5
Laniidae	4	0.09	1	11	1.10	2	2	0.48	2	16	1.38	2
Sturnidae	6	0.13	1	11	1.10	1	10	2.41	1	11	0.95	1
Ploceidae	2	0.04	1	1	0.10	1	4	0.96	1	4	0.34	1
Anatidae	7	0.16	2	3	0.30	1	2	0.48	1	3	0.26	1
Accipitridae	4	0.09	2	0	0.00	0	3	0.72	2	3	0.26	2
Falconidae	2	0.04	1	3	0.30	2	2	0.48	1	3	0.26	2
Phasianidae	11	0.25	2	13	1.30	2	17	4.10	3	17	1.46	3
Otidae	4	0.09	2	3	0.30	2	5	1.20	1	6	0.52	2
Scolopacidae	1	0.02	1	0	0.00	0	0	0.00	0	0	0.00	0
Strigidae	2	0.04	1	2	0.20	1	3	0.72	2	3	0.26	2
Upupidae	4	0.09	1	10	1.00	1	1	0.24	1	10	0.86	1
Picidae	1	0.02	1	0	0.00	0	0	0.00	0	0	0.00	0
Alaudidae	4	0.09	2	9	0.90	4	2	0.48	2	9	0.78	4
Columbidae	142	3.16	4	174	17.45	3	121	29.16	3	189	16.28	5
Pteroclididae	1	0.02	1	1	0.10	1	0	0.00	0	1	0.09	1
Meropidae	0	0.00	0	2	0.20	1	3	0.72	1	3	0.26	1
Ciconidae	1	0.02	1	0	0.00	0	0	0.00	0	0	0.00	0
Ardeidae	1	0.02	1	0	0.00	0	1	0.24	1	1	0.09	1
Emberizidae	1	0.02	1	0	0.00	0	2	0.48	1	2	0.17	1
Unident. passerine	14	0.31		15	1.50		3	0.72		15	1.29	
Recurvirostridae	0	0.00	0	0	0.00	0	3	0.72	2	3	0.26	2
Burhinidae	0	0.00	0	0	0.00	0	4	0.96	1	4	0.34	1
Cuculidae	0	0.00	0	0	0.00	0	2	0.48	1	2	0.17	1
Motacillidae	0	0.00	0	0	0.00	0	1	0.24	1	1	0.09	1
Apodidae	0	0.00	0	0	0.00	0	1	0.24	1	1	0.09	1
Charadriidae	0	0.00	0	0	0.00	0	1	0.24	1	1	0.09	1
Subtotal	262	5.84	32	328	32.90	31	285	68.67	37	411	35.40	45
Mammalia												
Carrion*	234	5.22	3	28	2.81	5	15	3.61	3	29	2.50	5
Leporidae	3.968	88.43	2	632	63.39	1	106	25.54	2	705	60.72	2
Erinaceidae	. 1	0.02	1	1	0.10	1	0	0.00	0	1	0.09	1
Muridae	2	0.04	2	3	0.30	2	0	0.00	0	3	0.26	2
Canidae	0	0.00	0	0	0.00	0	3	0.72	1	3	0.26	1
Subtotal	4,205	93.72	8	664	66.60	9	124	29.88	6	741	63.82	11
Amphibia												
Bufonidae	2	0.04	1	0	0.00	0	0	0.00	0	0	0.00	0
Subtotal	2	0.04	1	0	0.00	0	0	0.00	0	0	0.00	0
Reptilia												
Colubridae	5	0.11	1	1	0.10	1	3	0.72	1	5	0.43	1
Lacertidae	13	0.29	1	4	0.40	1	3	0.72	1	4	0.34	1
Subtotal	18	0.40	2	5	0.50	2	6	1.45	2	9	0.78	2
Total	4,487		43	997		42	415		45	1161		58
Levins' index	1.276			2.287			5.267			2.488		
Levins' index stand	0.011			0.067			0.164			0.051		

* Includes Ovis aries, Sus scrofa, Ovis musimon, Cervus elaphus, Bos taurus and Capra hircus.

ences (χ^2_4 = 1552, *P*<0.0001; Fig. 1). Remains and pellets underestimated larger prey (>601 g) and overestimated small and medium-sized prey (<300 g and 301–600 g, respectively).

A total of 72 taxa were identified: 43 as prey delivered, 42 in pellets and 45 in remains. No significant differences were found among the prey categories (bird, mammals and amphibians/reptiles; $\chi^2_{4} = 0.948$, P = 0.917; Table 1). Of a total of 56 bird species identified, the direct observations of prev items delivered to the nest allowed for the identification of 32 (57.1%) species belonging to 20 families. Meanwhile, the pellets allowed a total of 31 (55.3%) bird species of 15 families to be identified. Remains allowed an identification of 37 (66.1%) bird species of 23 families. As for the mammals, of 13 species identified, the direct observation of prey determined eight (61.5%) species. Pellets made it possible to identify nine (69.2%) species, and remains allowed identifying seven (53.8%) species. Finally, of the 3 species of amphibians/reptiles identified, the direct observation of prey allowed three species (two amphibians and one reptile) to be identified, while only two species of reptiles were determined in pellets and remains. The mean number of identified species per detected family was not significantly different among the methods (Kruskal-Wallis test; H = 1.33, df = 2, P = 0.514). However, the greatest dietary breadth was indicated by the prey remains data (5.267; Table 1).

When grouped together, the four most representative categories of prey (Corvidae, Columbidae, Carrion and Leporidae), constituted 97.6% of the total prey in the observational data, 90.1% in the pellet data, and 77.1% in the remains data (Table 1). The three methods thus produced different estimates ($\chi^2_6 = 1356.66$, *P* <0.0001). Compared to the observational data, pellets and remains overestimated Corvidae and Columbidae species and underestimated Leporidae.

3.2. Comparison of pooled sample with prey delivered

Of the 1,161 remains that were identified in the pooled sample, 411 (35.4%) corresponded to mammals, 741 to birds (63.8%) and nine (0.8%) to reptiles. The three methods produced significantly

different estimates of prey delivered between observational data and the pooled pellet plus prey remains data ($\chi^2_2 = 2132.04$, *P* <0.0001). Hence the pooled data overestimated birds and underestimated mammals.

Also the frequency of prey-by-weight categories significantly differed between observational and the pooled pellet plus remains data (χ^2_4 = 1156.85, *P* <0.0001; Fig. 1). The pooled method thus underestimated large prey (>601 g) and overestimated small and medium-sized prey (<300 g and 301–600 g, respectively).

The pooled method allowed the identification of 45 bird species belonging to 24 families, 11 mammal species, and two reptile species (Table 1). The frequency of species identified was significantly higher by using the pooled method than by using the observational data for birds ($\chi^2_1 = 7.025$, P = 0.0080), but not for mammals ($\chi^2_1 = 3.47$, P =0.06) or for amphibians/reptiles ($\chi^2_1 = 1.20$, P =0.273). As shown by the pooled trophic diversity index (2.488), this method revealed a higher trophic diversity than the observational (prey delivered) method (1.276).

Finally, when the four most representative prey categories (Corvidae, Columbidae, Carrion and Leporidae) were grouped, the pooled vs. observational method produced statistically different results (χ^2_3 = 589.89, *P* <0.0001). The pooled method continued to overestimate Corvidae and Columbidae and underestimate Leporidae.

4. Discussion

Although the diet of the Spanish Imperial Eagle mainly consists of wild rabbits (Delibes 1978, González 1991), the application of the supplementary feeding programme – where the birds were fed rabbits (González *et al.* 2006) – has probably caused the direct observation method to overestimate Leporidae. Apart from being an artificial, additional prey supply, rabbits are an easy prey item to identify as compared to small birds and other prey that appears more frequently in remains or pellets. Nevertheless, we believe that the present comparison appears objective for assessing biases of different diet assessment techniques.

One problem with comparing techniques is the error associated with direct observational data

(Redpath et al. 2001) and that prev delivered to the nest may be unrepresentative of the diet (Newton & Marquiss 1982). For example, direct observations may become biased if an unrepresentative cross-section of the diet is transported to the nest, in turn affecting the accuracy of this method (Sonerud 1992). In our study, conspicuous prey items may have been overestimated. On the other hand, most of the unidentified prey items delivered are small prey - such as birds, a group that the remains and pellet methods clearly overestimated - which may explain the low estimate of dietary breadth produced by the direct observation method. Moreover, the Spanish Imperial Eagle generally delivers food items to the nest without beforehand preparing. Hence, biases related with large prey that had been dismembered and delivered to the nest in more than one visit are negligible.

The present results suggest that the three methods used to assess the diet of the Spanish Imperial Eagle produce significantly different diet width and compositional estimates, and that pooling pellets and prey remains do not significantly reduce these biases. Pellets, remains, and these two pooled all overestimated birds and underestimated mammals. Regarding the size of the prey, remains, pellets and the pooled data underestimated larger prey items and overestimated small- and mediumsized prey categories. A possible explanation may be that eagles might eat several small prey items upon capture and thus not bring them to the nest. Such small prey items would appear in pellets/remains, but would not be observed as being delivered to the nest. Likewise, if an eagle captures a larger previtem, it might eat part of it and bring the rest to the nest or deliver the prey directly to the nest and eat part by itself while feeding the chicks.

To reduce the biases that the pellet and prey remains methods create in assessing raptor diets, a combination of these techniques has been suggested (Simmons *et al.* 1991). Indeed, such pooled-data method has been applied in several raptor diet studies (e.g., Oro & Tella 1995, Marchesi *et al.* 2002, Sarasola *et al.* 2003). In addition, the method has been compared with the diet observation method (Collopy 1983, Mañosa 1994, Seguin *et al.* 1998, Redpath *et al.* 2001). Of these studies, only Redpath *et al.* (2001) found significant differences when comparing data from direct observations and from combined pellets and remains. The present results agree with this study, suggesting that such pooled data may not always be the best indirect method. However, despite the biases detected, the method that was closest to direct observations was pellet analysis. So, if direct observations are not possible for estimating the diet, it would be best to use this method independently without combining it with the analysis of remains.

In food remains, large prey items generally tend to be over represented and small prey items underrepresented (Redpath et al. 2001, Lewis et al. 2004). Surprisingly, in the present study mammals were underestimated in pellets and, above all, in prey remains. This could be because the conspicuousness and ease with which these prey items are observed leads to overestimates in the direct observation method. Moreover, large and pale remains can be detected more easily than small or dark items (Newton & Marquiss 1982, Rutz 2003). In addition, the time period during which remains accumulated in the nests before collection could produce biases (Tornberg & Reif 2007). In this respect, due to degradation and/or removal by scavengers, mammals and birds (Oro & Tella 1995), pellets and remains are likely to be biased towards food delivered towards the end of the breeding cycle. Thus, the collection of data via direct observations and pellet and remains methods may not have been strictly contemporaneous, and this may affect the validity of comparing the two types of dataset. In addition, larger prey items contain many larger bones that an eagle may not eat and the prey remains may be taken by scavengers, leading to their occurrence being underestimated. Finally, the conservative method that involves estimating the minimum number of prey items in remains and pellets, compared to prey delivered, probably increases these differences.

The present results suggest that different sampling techniques have remarkable limitations and biases. A combination of pellets and prey remains allows the observer to obtaining larger sample sizes easily and quickly. However, biases identified in the present study must be carefully considered when interpreting studies on raptor diets. In order to take the advantage of direct observations as a surrogate for the most objective diet method, the use of video cameras may facilitate the identification of small prey items to avoid these biases (e.g., Margalida *et al.* 2005, Tornberg & Reif 2007). Only with objective data, obtained from observed prey delivered to the nest, will it be possible to validate the use of alternative indirect methods.

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Ravinnonkäytön tutkimusmenetelmien virhelähteitä iberiankeisarikotkalla *Aquila adalberti*

Tutkimuksemme määrittelee ensimmäistä kertaa virhelähteet, jotka liittyvät eri ravinnonkäytön arviointimenetelmiin (suorat havainnot, pelletit, saaliin jäännökset sekä pelletit ja jäännökset yhdessä), joita on käytetty iberiankeisarikotkan ravinnonkäytön tutkimuksessa. Kun suoria havaintoja käytettiin pesälle tuodun ravinnon objektiivisimpana mittarina, tarkastellut kolme metodia – pelletit, jäänteet ja nämä kaksi yhdessä – yliarvioivat lintujen ja aliarvioivat nisäkkäiden osuutta saaliissa. Nämä metodit edelleen aliarvioivat isokokoisten (>601 g) mutta aliarvioivat pienten ja keskikokoisten (vastaavasti >300 g ja 301–600 g) saaliseläinten määrää. Jäänteet tuottivat laajimman arvion ravintokohteiden kirjosta.

Tuloksemme osoittavat, että nämä kolme menetelmää – joita on yleisesti käytetty iberiankeisarikotkan ravinnonkäytön arvioinnissa – antavat varsin erilaisia tuloksia, ja ettei yhdistettyä aineistoa (pelletit ja jäänteet) voi luotettavasti käyttää virheen pienentämiseen. Virheen suuruus vaihtelee huomattavasti saalisryhmittäin, eikä aineistomme perusteella ole mahdollista osoittaa sopivinta petolintujen ravinnonkäytön arviointimenetelmää. Havaitsemamme eri epäsuorien ravinnonkäytön arviointimenetelmien virheet tulisi huomioida luonnonhoidon ja -suojelun strategioita suunniteltaessa.

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