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Subcutaneous fat accumulation in Norwegian owls and raptors

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The mean subcutaneous fat deposition (MFS) found in dead diurnal raptors and owls collected in Norway in 1987–92 was compared to detect possible overall and intra- and interspecific seasonal differences. In general, the relative fat deposition rate was correlated with body size ($P < 0.001$), and was highest in winter ($P = 0.01$) and in females ($P = 0.02$). After correcting for the size effect, species-specific differences were still present ($P = 0.000$), but the effect of sex disappeared ($P = 0.34$). We propose that the relative rate of fat deposition in northern Palaearctic owls and raptors reflects adaptations to resist starvation balanced against the demands for high agility and low flying costs. This trade-off probably varies between breeding and non-breeding seasons, sexes, and species with different migratory and hunting habits.

1. Introduction

Some bird species are known to periodically have reserves of body fat (Helms 1968, King 1972). This is explained by a need to maintain good physiological condition prior to periods when food is generally limited and/or in association with migration and reproduction (Lack 1954, Blem 1976, O'Connor 1980). Thus, it may be valuable to measure the fat-storing ability of an organism when interpreting ecological aspects of associated groups of species, a particular species, or behavioural adaptations within a species. Present knowledge about such aspects of bird physiology stems mainly from studies of passerines (Marsh & Dawson 1989, Grubb & Pravosudov 1994), and some aquatic species (Ebbinge & Spaans 1995), and little is known about the way many other bird species and orders physiologically adapt to the environment. Data are particularly limited in the case of many birds of prey (Newton 1979, Hirons et al. 1984), probably because many owl and raptor populations are small and widely dispersed, and also totally protected, making the collection of sufficient samples difficult. However, it may be envisaged that raptorial birds which are totally or seasonally resident in Fennoscandia, where the climate is partly harsh, and which mostly depend upon vertebrates that occur at irregular intervals (Hansson & Henttonen 1985), may evolve starvation-resisting tactics — fat storing perhaps being the most plausible one.

A collection of *Strigiformes* and *Falconiformes* accidentally killed in Norway allowed us to investigate the degree of subcutaneous fat accumulation in terms of species, sexual and seasonal differences. The results are discussed in relation to body size and behavioural aspects.

2. Material and Methods

After eliminating individuals which had died of hunger and/or whose sex or date of death could not be determined with certainty, the material consisted of 963 carcasses of five species of raptors and 797 carcasses of seven species of owls collected between 1987 and 1992. The birds had generally died after colliding with man-made installations (Bevanger & Overskaug 1995). Information was available on where and when each carcass was found. The sex was determined by dissection and examination of the sex organs (e.g. Overskaug et al. 1995). The relative amount of subcutaneous fat was categorised visually as Fat Scores (FS) on a scale from 1 (no fat) to 6 (very much fat). The specimens were divided into summer (March–August) and winter (September–February) groups. The Appendix gives the raw data of fat scores, season, species and sex.

Classification of fat scores by visual observation has previously been used to estimate the condition of birds (Helms & Drury 1960, Kaiser 1992), including predators (e.g. Hirons et al. 1984). However, a visual fat-code index is subjective and analysis of such data should be treated with care (Rogers 1991, Greenwood 1992). We reduced this problem by having only one person evaluate the fat scores for the entire sample. When investigating relationships between intra- and interspecific dif-

Table 1. **I. General log-linear models** to show the effect of the species (SP), body length (minus tail length) (LE), season (SW) and sex (SEX) on the fat score (FS) distribution. C is the model constant. The significance of an interaction between a classifying variable and the FS (a dependent variable) is tested as the significance of the overall-fit model for no interaction (in contrast to the totally saturated model with all possible higher- and lower-order interactions included, and which by definition has a perfect model fit). **II. Log-linear regression models** where the possible ordinal ordering of FS is modelled by covariates between each of the classifying variables (SW, SEX and LE) and the FS. A regression model that did not include species-specific differences in FS that are not related to the effect of body length **(A)** did not fit with the data. When the interaction FS × SP is added to the model **(B)**, a very good model fit is achieved. The significance of the covariate parameters of model B are shown lower in the table. The coefficient values (coeff.) show that the FS values are positively correlated with body size, and birds from the winter (internal code = 1) on average had higher FS values than birds from the summer (code = 2). After entering LE as a classifying variable, sex no longer had a significant effect on the FS.

Expression	Chi-square[1]	DF	P
I. General log-linear models			
(Saturated model)			
SP × SEX × SW × FS	(0.00)	(0)	(1.00)
Species effect excluded			
C + SP × SEX × SW + FS × SEX × SW	617	200	0.000
Seasonal effect excluded			
C + SP × SEX × SW + FS × SEX × SP	146	110	0.012
Sexual effect excluded			
C + SP × SEX × SW + FS × SP × SW	142	110	0.020
II. Log-linear regression models			
A. No species-specific interaction with FS included			
C + SP × SEX × SW + FS + (FS × LE) + (FS × SW) + (FS × SEX)	420	212	0.000
B. Species-specific interaction with FS included[2]			
C + SP × SEX × SW + FS·SP + (FS × LE) + (FS × SW) + (FS × SEX)	120	162	0.994
Interaction parameters (covariates)	Coeff.	Z	P
Body length (mm)			
(FS × LE)	0.0078	4.96	0.000
Season (1 = winter, 2 = summer)			
(FS × SW)	– 0.1860	– 4.52	0.000
Sex (1 = male, 2 = female)			
(FS × SEX)	0.0477	1.01	0.32

[1] Likelihood ratio chi-square. [2] Species-specific effect independent of the effect of body length.

ferences in behaviour, physiology or morphology and ecological variables, it may be necessary to remove the effects of the confounding variable, body size (Clutton-Brock & Harvey 1979, Calder 1984). Thus, we compared fat deposition in the species investigated relative to their body size, using as a scale the body length for each sex (Cramp & Simmons 1980) minus the tail length (Dement'ev et al. 1951).

In the initial tests (Table 1), we conducted an overall log-linear analysis. Differences in the distribution of FS between different species, sexes and seasons were tested for by comparing the overall model fit with and without the interaction of FS with each of the selected factors (Table 1: I). All interactions between the classifying variables were included in the models so that the only unsaturated link was between the FS and one factor each. Since all three factors interacted significantly with the FS and the FS could be ranked due to its ordinal nature (from 1 to 6), and since the mean FS (MFS) seemed to be positively correlated with body length, a logistic regression model was generated (Table 1: II):

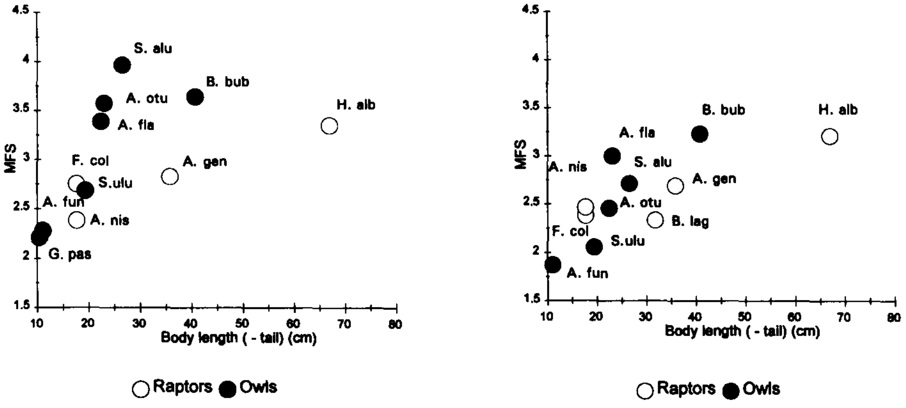
$$SEX \times SP \times SW + FS \times SP + (SEX \times FS) + (LE \times FS) + (SW \times FS) + C,$$

where SEX × SP × SW includes all main effects, second- and third-order interactions between the factor sex (SEX), species (SP) and summer/winter (SW). FS × SP include the second-order interaction between the species and the fat score distribution that is not explained by body length. The main effects of (SEX × FS), (LE × FS) and (SW × FS) are the covariates between the FS and sex, body length (LE) and season, respectively. The covariates ("logistic regression coefficients") reveal the linear relationship between the FS and the independent variables (Norusis 1994). C is a model constant. The second-order interaction FS × SP was included in the logistic regression model (Fig. 1: B) because it considerably improved the overall fit (from $P = 0.000$ to $P = 0.994$). Z values were generated for the significance of the parameter values, where numeric z values > 1.96 ($P < 0.05$) indicate significant deviations from 0. In the log-linear models, each cell was weighed equally; species with low sample size had the same statistical weight as species represented by large samples. Because of a relatively high rate of empty cells (54 sampling zeros out of 264 defined cells (20%), the accurate parameter values and P values should be treated with some caution.

To clarify species-specific adaptations we supplemented the log-linear models with univariate statistics (Table 2). If these univariate tests agreed with the overall result of the log-linear models, they would provide further confirmation of the overall result. Because of the effect of seasons and (possibly) sex on the FS distribution, the analysis was divided into separate sexual and seasonal groups. In the test above the species level we used the mean fat score (MFS) as an index based upon the mean of the FS in subsamples of at least 9 observations. Furthermore, deviations in the MFS ($DMFS\ (A - B) = MFS_A - MFS_B$)) between season and sex were used to test differences in the MFS between related cases. Spearman's Rank Correlation coefficient (r_s) was used to test for correlation between the MFS and body size, the sexes being considered separately (Fig. 1). In pairwise tests, the Wilcoxon Matched-Pairs Signed-Ranks-test was used for related cases. The Mann-Whitney U-test was used to test for seasonal or sexual differences in median FS on the species level. However, due to the varying sample size, occurrences of species showing significant seasonal or sexual differences may be as much a result of sample size as an effect of the strength of the group difference. Nevertheless, significant differences within a species do at least reflect a real difference, which may have species-specific interest. A sign test was used to present an overall tendency with all the raptor and owl species included. All tests are two-tailed.

3. Results

The distribution of fat scores was affected by all three factors: species, season and sex (Table 1). A linear regression model with the linear effect of size, season and sex gave a very good model fit after the species-specific interaction with FS was included (Table 1: II B). The linear interactions with FS showed a highly significant positive correlation with body length, and birds from the winter were significantly fatter than birds from the summer. However, the sexual-specific effect on FS disappeared ($P = 0.32$ versus 0.02 in the general model) after the body-size term was included in



A. Males, winter

B: Males, summer

C. Females, winter

D. Females, summer

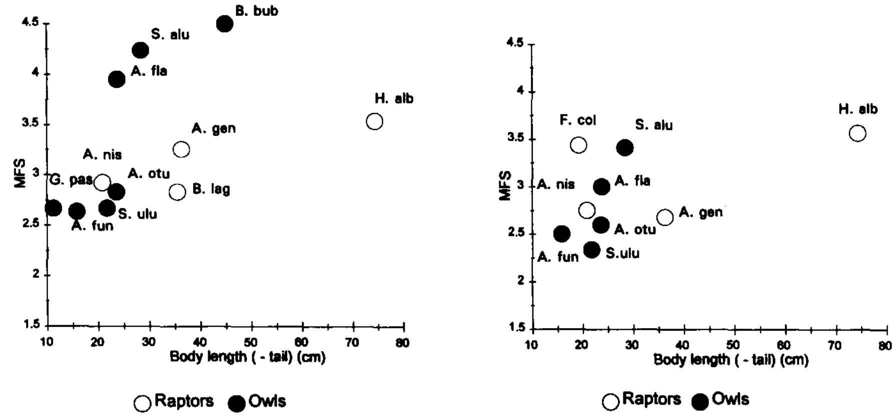


Fig. 1. MFS values correlated (Spearman's rank correlation coefficient) with body size (body length with tail length subtracted) for males and females in winter and summer. Because of the inadequate sample sizes of raptor species, correlation coefficients are only shown for owls. Males, winter; $r_s = 0.964$, $p < 0.02$, $n = 7$, summer; $r_s = 0.943$, $p = 0.02$, $n = 6$. Females, winter; $r_s = 0.964$, $p < 0.02$, $n = 7$, summer; $r_s = 0.900$, $n = 5$. Species annotations: H. alb: *Haliaeetus albicilla*, B. lag: *Buteo lagopus*, A. nis: *Accipiter nisus*, A. gen: *Accipiter gentilis*, F. col: *Falco columbarius*, S. alu: *Strix aluco*, S. ulu: *Surnia ulula*, G. pas: *Glaucidium passerinum*, A. fun: *Aegolius funereus*, A. fla: *Asio flammeus*, A. otu: *Asio otus*, B. bub: *Bubo bubo*.

the model. The tendency for females to be fatter than their male conspecifics thus seemed to be a function of their larger body size. There was also a significant interaction between species and FS, showing that different species still have species-specific fat depositing rates in addition to the general effect of body size.

In the univariate tests, a positive relationship between the MFS and body size was present for both raptor and owl species, for both sexes and for both seasons (Fig. 1A–D). In owls, all testable ($n > 5$) correlations were significant (Fig. 1A–C). In general, females were fatter than males, and birds from the winter were fatter than birds from the summer (Table 2). Thus, the univariate tests confirmed the result of the log-linear models. Within species, Goshawk *Accipiter gentilis* and Sparrow Hawk *Accipiter nisus* females were fatter than males in winter (Table 2). Female Sparrow Hawks remained fatter than males in summer. Similarly, Merlin *Falco columbarius* females were fatter than males in summer. Tawny Owl

Table 2. Mean fat score (MFS) differences caused by different sex or season. Missing values are caused by inadequate sample sizes ($n < 9$). Significant deviations from unity in medians between groups within species tested by the Mann-Whitney U-test are abbreviated by * ($P < 0.05$), ** ($P < 0.01$) or *** ($P < 0.001$). The original MFS values are presented in the Appendix.

Species		Seasonal variation (MFS$_{winter}$ – MFA$_{summer}$) Male	Female	Sexual variation (MFS$_{female}$ – MFA$_{male}$) Summer	Winter
Raptors					
Haliaeetus albicilla		0.14	−0.03	0.36	0.19
Accipiter nisus		0.06	0.17	0.37**	0.48**
Accipiter gentilis		0.15	0.58*	0.00	0.43*
Falco columbarius		0.28	−0.66	0.97**	0.03*
Owls					
Strix aluco		1.26***	0.83**	0.70	0.27
Surnia ulula		0.64*	0.35	0.28	−0.01
Aegolius funereus		0.41	0.14	0.63	0.36
Glaucidium passerinum		–	–	–	0.46
Asio flammeus		0.57	0.95	0.00	0.38
Asio otus		0.93*	0.23	0.14	−0.56
Bubo bubo		0.41	–	–	0.86
Sign test	+	10	7	7	9
(All species)	0	0	0	2	0
	–	0	2	0	2
	P	0.002	0.18	0.02	0.07
Wilcoxon's MPR-test	P	0.03	0.04	0.07	0.24
(Owls only)	n	6	5	5	8

Strix aluco and Tengmalm's Owl *Aegolius funereus* females stored more fat than males in summer. Seasonal intrasexual differences in raptors were demonstrated by the Goshawk where the female was fatter in winter than in summer (Table 2). Both sexes of the Tawny Owl accumulated more fat in winter than in summer, and Hawk Owl *Surnia ulula* and Long-Eared Owl *Asio otus* males stored more fat in winter than in summer (Table 2).

4. Discussion

4.1. General patterns

A correlation between fat accumulation and body size (Fig. 1) confirms the impression that larger species are more capable of storing fat than smaller ones (Pitts & Bullard 1968). Furthermore, the fat accumulation practised by some of the raptorial species investigated here should probably in general be seen as a long-term survival strategy to buffer periods of starvation or thirst during residency — the "capital model" of Drent and Daan (1980) — in contrast to the more short-term accumulation seen, for instance, in smaller and often more migratory species — the "input model" of Drent and Daan (1980). With the possible exceptions of the Merlin (Haftorn 1971) and Long-Eared and Short-Eared Owls *Asio flammeus* (Mikkola 1983), the species considered here only migrate in a step-wise manner (Cramp & Simmons 1980). Nonetheless, they may still be found in a northern environment in winter; indeed, they would not otherwise have been present in this material.

Because the survival of raptorial birds is probably closely related to agility, we may expect fat accumulation to be very well balanced between the need for an energy reserve to buffer periods when prey capture rates are low (high fat level) and the need for a high flying performance (low fat level). The result of this study strongly suggests that seasonal and morphometric factors influence the rate at which raptorial birds in northern temperate areas accumulate fat reserves. Large birds accumulate relatively larger fat deposits than smaller ones, and winter fat reserves are generally larger than summer ones. An important explanation for larger birds being fatter than smaller birds may be that from a cost-benefit point of view it is not adaptive for small species to accumulate large amounts of fat, for instance because of the need for great mobility in connection with hunting (see Pennycuick (1975) and Rayner (1982) regarding the proportional increase in body weight and cost of flying). High vigilance is probably also important to avoid predation from larger birds of prey (Newton 1979, Hakkarainen & Korpimäki 1991) and other predators (Sonerud 1985). In addition, due to the higher mass-specific metabolic needs of small bodies compared with large ones, the reserves will last a much shorter time for small raptors than for large ones. This may also be illustrated by the fact that the smallest raptorial birds overwintering in the boreal winter, the Pygmy Owl *Glaucidium passerinum* and the Tengmalm's Owl, store prey in winter (Mikkola 1983, Korpimäki 1987), thereby avoiding an impossible dilemma by adopting an alternative energy-storing strategy.

The trend towards a higher fat deposition rate in winter than in summer may reflect the situation that in Norway prey availability may be so low outside the breeding season that it is beneficial to increase the energy reserves in the beginning of winter, as part of a strategy for winter-survival. On the other hand, the generally lower fat deposition in summer may reflect a higher prey-capture–maximising/flying-cost–energy-minimising tactic then. Low fat deposition in summer seems to be especially expressed among males, perhaps as a result of the burden of feeding the brooding female, a practice frequently found in raptors (e.g. Cramp & Simmons 1980). The larger body size of the females compared with males may therefore be an advantage during the energy-expenditure reproduction period. The positive effect of the greater body size of females for their ability to accumulate fat is illustrated by the fact that even though females had a higher overall fat accumulation rate than males, this capacity only seemed to be a function of the larger body size; in general, females seemed to be no fatter than males when the figures were corrected for body size.

4.2. Species- and sex-specific patterns

In addition to the effect of body size, behavioural differences between sexes may play a part in the ability to store fat. For example, in Sparrow Hawks, where females are fatter than males throughout the year, the male feeds the female in the early breeding season and is also reported to hunt quite far from its nest at times (Newton 1979: 41). This may contribute to the difference in fat storage between the sexes in this species. The sexes also behave differently during the non-breeding season, females tending to stay and hold a territory while males move around more (Moritz & Vauk 1976). These behavioural characteristics probably favour the larger body size and greater ability to store fat seen in females compared with males. On the other hand, Goshawk females only seem to be fatter than males in winter (but see Marcström & Kenward 1981). However, some behavioural aspects also contrast with those mentioned above for the Sparrow Hawk. The Goshawk starts breeding early in spring, adults and young remain together for a long time after the postfledgling period and females share hunting with males to feed the offspring (Haftorn 1971). This investment may not favour the building up of body fat reserves in either of the sexes of the Goshawk in summer. The difference between the sexes in winter may be explained by the females alone establishing and maintaining the nesting territory, and consequently moving less than the males (Mueller & Berger 1968, Haukioja & Haukioja 1970).

Among owls, Tawny and Tengmalm's Owl females store more fat than males in summer. Like raptors, the females of these species remain at the nest throughout the spring and are fed by their partners (Mikkola 1983), thus increasing their opportunity to stay in good condition compared with males (e.g. Hirons 1985). Korpimäki (1989) and Hakkarainen and Korpimäki (1991) also suggest that selection takes place for small Tengmalm's Owl males that are agile and good hunters. Perhaps selective pressure for limited body weight is also present in male Tawny Owls, which it has been shown may hunt more agile prey than females (Overskaug et al. 1995). Sex-specific adaptations may also be present in Hawk and Long-Eared Owls, the males being fatter in winter than in summer. For example, because the females of those species show a greater tendency to move from their breeding range than males (Byrkjedal & Langhelle 1986, Overskaug & Kristiansen

1994, but see also Lundberg 1979), there may be no advantages in having higher fat levels than the more resident males.

Considerable body fat accumulation in winter in both sexes of the Tawny Owl may be connected with them remaining in their territories throughout the year, partly in cold environments where food is limited (Southern 1970, Korpimäki 1986). However, a certain degree of fat storage, or of increase in mid-winter weight that indicates fat storage, is also reported from southern parts of the range of the species (Baudvin & Dessolin 1992). Nevertheless, the particularly early breeding season found in this species, in Norway even in winter when food is limited (Byrkjedal & Langhelle 1985, Helle 1986), may contribute to its need for large fat reserves. Individuals that are in good condition normally also raise more offspring, and Wallin (1987) observed that the level of offspring defence was positively correlated with the body mass of females. We propose that ability to store subcutaneous fat during autumn and winter plays a key role in this selection for heavier individuals in the female Tawny Owl, but that the male may be subject to a selection feature that is more designed to balance the need for fat reserves in winter as opposed to the need for being a good hunter in summer.

4.3. Conclusions

Apart from some general patterns, such as larger birds accumulating relatively more body fat and accumulation of more body fat in winter compared with summer, the levels of fat accumulated in an assortment of predatory bird species wintering in the same northern area are subject to substantial intraspecific variability. Clearly, the selective forces and associated limitations that determine the degree of fattening are complex and current models that attempt to predict optimal levels of fat (e.g. Lima 1986) appear too simplistic to explain the variability that exists in the northern Palaearctic owls and raptors investigated here. We propose that both body size and species-specific behavioural characteristics may play roles in this context.

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Selostus: **Norjalaisten pöllöjen ja päivällä saalistavien petolintujen ihonalaiset rasvakeräytymät**

Norjassa vuosina 1987–92 keräiltyjen kuolleiden päivällä saalistavien petolintujen ja pöllöjen keskimääräisiä ihonalaisia rasvavarastoja (MFS) vertailtiin mahdollisten yleisten sekä lajikohtaisten ja lajien välisten vuodenaikaisten erojen paljastamiseksi. Yleisesti ottaen suhteellisen rasvavaraston määrä oli suhteessa ruumiin kokoon, ja se oli korkein talvella ja naarailla. Kokoeron vaikutuksen korjaamisen jälkeen lajikohtaisia eroja oli edelleen havaittavissa, mutta sukupuolen vaikutus katosi. Me oletamme, että pohjoisten alueitten pöllöjen ja petolintujen suhteellisten rasvavarastojen määrä heijastaa kykyä vastustaa nälkiintymistä, vastapainona korkean liikkuvuuden ja matalien lentokustannusten vaatimuksille. Tämä "kaupanteko" vaihtelee todennäköisesti pesimimiskauden ja pesimimiskauden ulkopuolisen ajan välillä, sukupuolten välillä ja sellaisten lajien välillä, joilla on erilaiset muutto- ja metsästystavat.

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Appendix. Fat Score raw data. Each specimen was rated on a scale of increasing fatness ranging from 1 (no fat) to 6 (very much fat). This table summarises the number of specimens in each Fat Score (FS) category in subsamples of birds from a known season and whose sex was determined. The Mean Fat Score (MFS) was calculated and used in the analyses of subsamples containing 9 or more specimens. Winter: September–February. Summer: March–August.

	Season	Sex	MFS	FS-1	FS-2	FS-3	FS-4	FS-5	FS-6	N_{total}
Haliaeetus albicilla	Winter	F	3.54	0	4	1	5	3	0	13
		M	3.35	2	3	3	5	4	0	17
	Summer	F	3.57	1	2	2	6	3	0	14
		M	3.21	1	3	8	5	2	0	19
Buteo lagopus	Winter	F	2.83	5	2	1	1	0	3	12
		M	–	1	0	0	0	2	0	3
	Summer	F	–	1	2	0	3	1	0	7
		M	2.62	1	8	1	2	0	0	12
Accipiter nisus	Winter	F	2.92	12	39	49	32	10	0	142
		M	2.44	17	54	40	13	2	0	126
	Summer	F	2.75	11	44	32	28	4	0	119
		M	2.38	16	51	21	16	1	0	105
Accipiter gentilis	Winter	F	3.25	14	17	22	27	22	0	102
		M	2.83	24	33	21	27	12	3	120
	Summer	F	2.68	8	12	10	5	5	0	40
		M	2.38	5	16	11	5	4	0	41
Falco columbarius	Winter	F	2.78	0	6	0	2	1	0	9
		M	2.75	3	4	5	2	2	0	16
	Summer	F	3.44	1	1	6	6	2	0	16
		M	2.47	5	13	7	3	2	0	30
Strix aluco	Winter	F	4.24	8	17	16	16	27	38	122
		M	3.97	7	10	10	6	7	21	61
	Summer	F	3.41	13	19	10	7	9	17	75
		M	2.71	10	22	6	5	5	4	52
Surnia ulula	Winter	F	2.67	4	30	22	6	5	0	67
		M	2.69	2	26	17	6	2	1	54
	Summer	F	2.33	2	11	2	3	0	0	18
		M	2.71	10	22	6	5	5	4	52
Aegolius funereus	Winter	F	2.64	1	10	8	2	1	0	22
		M	2.28	10	12	8	6	0	0	36
	Summer	F	2.50	1	9	3	3	0	0	16
		M	1.87	10	15	6	0	0	0	31
Glaucidium passerinum	Winter	F	2.67	1	7	7	3	0	0	18
		M	2.21	4	7	8	0	0	0	19
	Summer	F	–	0	2	3	0	0	0	5
		M	–	0	4	3	0	0	0	7
Asio flammeus	Winter	F	3.95	1	4	2	5	4	4	20
		M	3.57	0	5	7	3	4	2	21
	Summer	F	3.00	2	3	4	1	3	0	13
		M	3.00	1	1	7	3	0	0	12
Asio otus	Winter	F	2.83	3	6	4	2	2	1	18
		M	3.38	0	4	4	2	2	1	13
	Summer	F	2.60	2	3	3	1	1	0	10
		M	2.46	6	9	5	1	2	1	24
Bubo bubo	Winter	F	4.50	0	2	1	1	5	3	12
		M	3.64	1	2	4	3	2	2	14
	Summer	F	–	0	0	1	1	2	1	5
		M	3.23	3	2	2	1	5	0	13