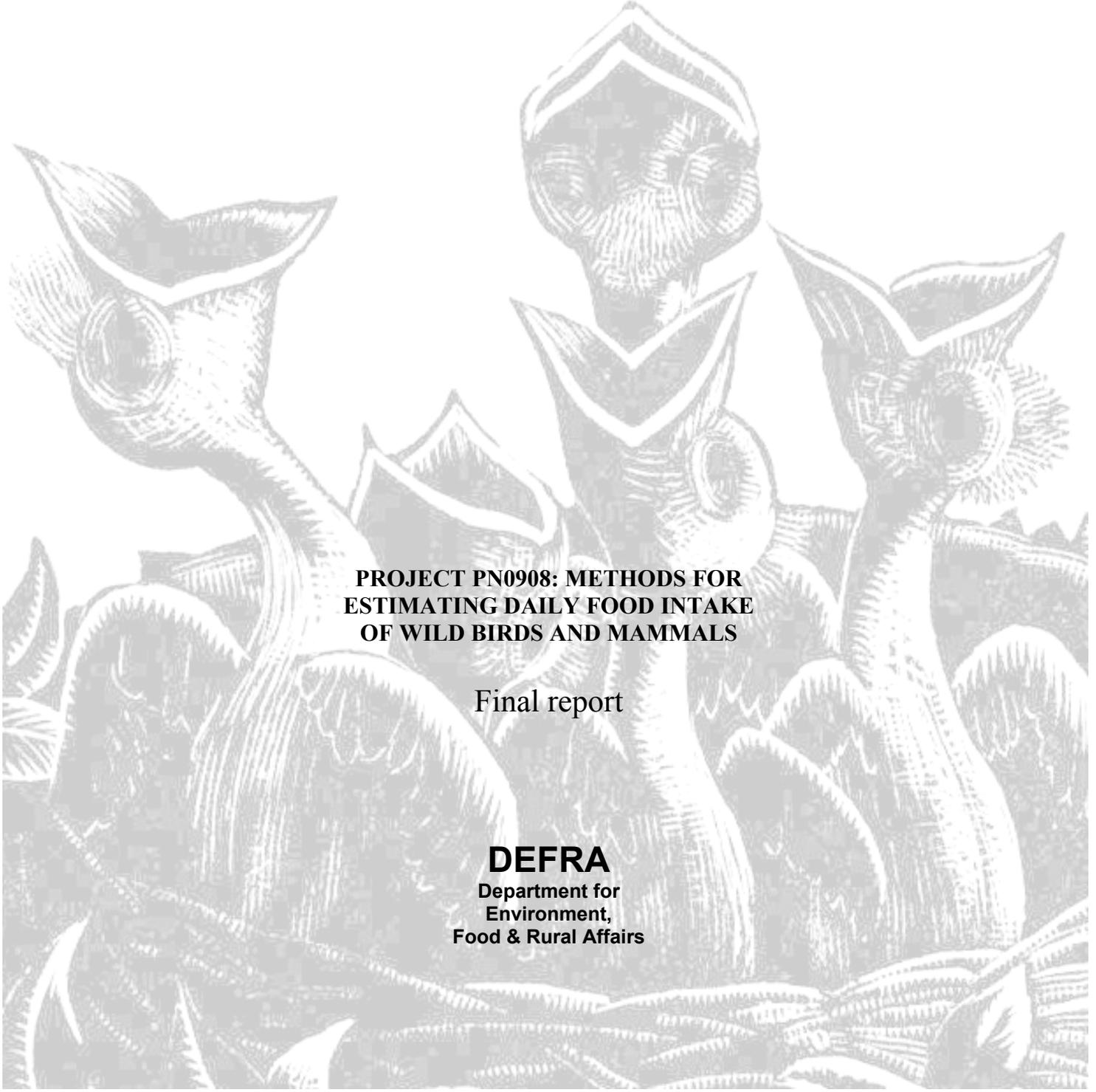




CENTRAL SCIENCE LABORATORY

SCIENCE SERVING AGRICULTURE, FOOD AND THE ENVIRONMENT



**PROJECT PN0908: METHODS FOR
ESTIMATING DAILY FOOD INTAKE
OF WILD BIRDS AND MAMMALS**

Final report

DEFRA
Department for
Environment,
Food & Rural Affairs

Report to:

Ingrid Meakin
Arable Crop Sciences and Pesticide Safety
DEFRA
Cromwell House
Dean Stanley Street
Westminster
London SW1 3JH

Paul Adamson
Pesticides Safety Directorate
Mallard House
3, Peasholme Green
York YO1 2PX

Simon Hoy
Pesticides Safety Directorate
Mallard House
3, Peasholme Green
York YO1 2PX

CSL Project Leader:

Dr A D M Hart
Central Science Laboratory
Sand Hutton
York
YO41 1LZ

**PROJECT PN0908: METHODS FOR ESTIMATING
DAILY FOOD INTAKE OF WILD BIRDS AND MAMMALS**
Final report

D Crocker, A. Hart,
J. Gurney and C. McCoy
Central Science Laboratory
July 2002

Summary

If the risks to non-target wildlife posed by pesticides and other contaminants of their foods are to be properly assessed then we need good quantitative information about wildlife daily food intake. Such information is difficult to obtain. There is however increasing information on the Daily Energy Expenditure (DEE) of free-ranging birds and mammals. When combined with information on the energetic values of wildlife foods and the efficiency with which they are assimilated, it is possible to estimate the likely daily food intake. We have reviewed data on DEE of wild birds and mammals and data on their digestive efficiency. We have collated data on energy and moisture values of wildlife foods. For 82 scenarios of UK birds and mammals feeding on different foods, we have calculated their likely daily food intake. We discuss advantages and limitations of the method and outline how the data may be used in deterministic and probabilistic risk assessments to predict food intake.

Introduction

Wildlife feeding among crops will be exposed to pesticides applied there. Given knowledge about residue levels, if we know how much they eat, we can calculate their likely exposure. Unfortunately, it is rarely possible to follow a wild bird or mammal closely enough to monitor what foods it eats, in what quantities. But it is possible (using isotopic tracers) to measure how much energy a wild animal uses in a day. If we know what the animal eats, the energy value of the food, its moisture content and how efficiently the animal digests it, we may calculate how much of the food it must find each day to satisfy its daily energy expenditure. Estimates of this type published by Nagy (1987) are widely used in ecological risk assessment.

Currently the European Plant Protection Organisation suggests that daily food intake may be estimated by using Nagy's equations or by using a simple rule of thumb in which the dry weight daily food intake of animals weighing less than 100g is approximately 30% of their bodyweight, and 10% for heavier animals (EPPO, 1994). Since Nagy's original publication, energy requirement studies have been published for a substantial number of additional species and Nagy himself has recently updated and revised his estimates (Nagy 1999). Also, Nagy's estimates relied on very limited information on food energy and moisture contents and assimilation efficiencies, and did not differentiate between food types. The objectives of this study were therefore: 1) to review the sources of information for estimating daily food intakes of wild birds and mammals and 2) to produce improved equations and estimates tailored to the needs of risk assessment.

Methods

Daily Energy Expenditure (DEE)

Although it is rarely possible in the field to follow an animal all day and to monitor what it eats and how much, there are biochemical means of estimating the energy

requirements of free-living animals. The most widely used is the Doubly-Labelled Water (DLW) method). An animal is caught, injected with isotopically labelled water, re-caught at a later date and a blood sample taken to determine the relative turn-over of the hydrogen and oxygen isotopes. From this a figure for CO₂ production can be calculated and in turn an estimate made of daily energy requirements. The advantage of this method is that it reveals the energy expenditure of an animal living in its natural habitat engaging in its normal activities and feeding on its normal foods. The DLW technique has been in common use in studies of wildlife energetics since the 1980s. A review by Nagy (1987) showed that there was a very good correlation between a species' average mass and the amount of energy it burns. Predictably, the bigger the bird or mammal species the more food it needs.

We reviewed the more recent literature on metabolic rate of free-living birds and mammals, and generated a new set of allometric equations linking body weight with Daily Energy Expenditure. Estimates of field metabolic rates, from studies using Doubly-Labelled Water isotopes, were found for 96 bird species and 73 mammal species.

Moisture and energy content of foods

We collated information on the energy and moisture contents of various wildlife foods. More than 2000 measurements of potential wildlife foods were grouped into 15 broad categories.

Assimilation efficiency

Some food passes through the gut unabsorbed to emerge as faeces. The true energy value of a food is given by the energy content of the food minus the energy value of the faeces. Therefore, in calculating the likely food intake we need to take account of different species' assimilation efficiencies for different foods. We collated data on the efficiency with which wildlife digest foods.

Estimation of average daily food intake

The final step was to use the above information to estimate average daily food intake. For a species of a given weight we may use our allometric equations to predict its daily energy expenditure. Knowing the energy value and moisture content of its typical foods, and the efficiency with which it digests them, we may calculate the average amount of food it is likely to eat in a day using the following equation

Equation 1

$$\text{Daily Food Intake (wet g)} = \frac{\text{Daily Energy Expenditure (kJ)}}{\text{Energy in Food (kJ/g)} \times (1 - \text{Moisture}) \times \text{Assimilation Efficiency}}$$

where moisture and assimilation efficiency are proportions between 0 and 1.

Results

Daily Energy Expenditure

For both birds and mammals there was a strong relationship between body weight and DEE. As previously reported (Nagy, 1987, 1999), there were significant differences between taxonomic groups and between species occupying different habitats.

Therefore separate equations were calculated for passerines, sea birds, desert birds, hummingbirds and others. Mammals were similarly divided into non-eutherians, desert mammals, sea mammals and terrestrial mammals. The equations are presented in Table 1 and Table 2 and relationships may be seen in Figure 1 and Figure 2.

Table 1. Birds. Relationship between body weight (g) and Daily Energy Expenditure (DEE (kJ)) in birds for selected groups of avian species. The general form of equation is: $\text{Log}(\text{DEE}) = \text{Log } a + b \times (\text{log Body weight})$. Insert $\log_{10} a$ and b from the table to obtain the specific equation for the relevant species group. Also shown are the standard errors for a and b (SE), the number of species in each group (N), and the proportion of variation explained by each equation (r^2).

Group	Log₁₀ a	SE Log₁₀ a	b	SE b	N	r²
Desert	0.6107	0.1727	0.7299	0.0663	7	0.95
Hummingbirds	0.7495	0.0822	1.2064	0.1090	5	0.97
Other	0.6768	0.1896	0.7723	0.0861	11	0.89
Passerine*	1.0017	0.0647	0.7034	0.0503	38	0.84
Seabird	1.1482	0.1022	0.6521	0.0356	35	0.91
all birds	1.0220	0.0392	0.6745	0.0180	96	0.94

*excluding marine and desert passerines

Table 2. Mammals. Relationship between body weight (g) and Daily Energy Expenditure (DEE (kJ)) in mammals for five groups of mammalian species. The general form of equation is: $\text{Log}(\text{DEE}) = \log a + b \times (\text{log Body weight})$. Insert $\log_{10} a$ and b from the table to obtain the specific equation for the relevant species group. Also shown are the standard errors for a and b (SE), the number of species in each group (N), and the proportion of variation explained by each equation (r^2).

Group	Log₁₀ a	SE Log₁₀ a	b	SE b	N	r²
Non-eutherians	1.0232	0.0749	0.5814	0.0251	19	0.97
All eutherians	0.6794	0.0445	0.7646	0.0173	54	0.97
Desert eutherians	0.5120	0.0625	0.7843	0.0290	18	0.98
Marine eutherians	2.4203	0.7592	0.4266	0.1567	6	0.56
Other eutherians*	0.8459	0.0526	0.7050	0.0250	30	0.96
All mammals	0.7401	0.0467	0.7204	0.0174	73	0.96

* excluding desert and marine eutherians

Figure 1. Relationship between log daily energy expenditure against log bodyweight for 96 bird species

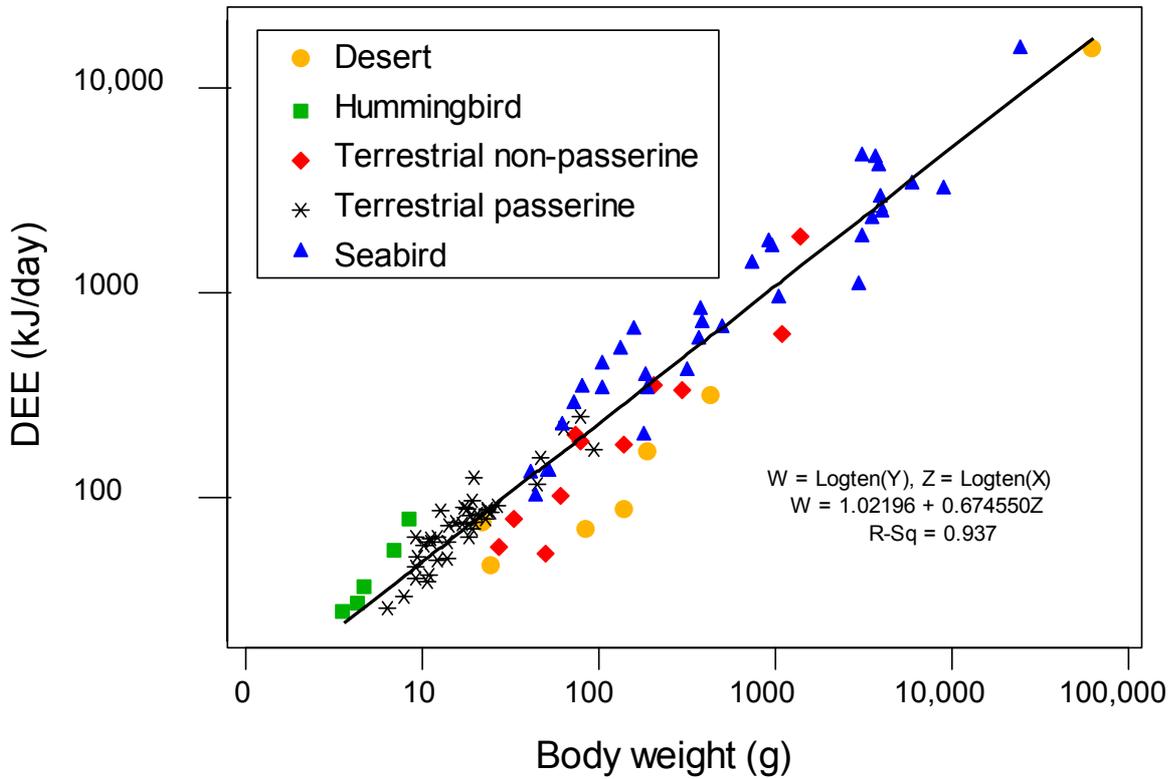
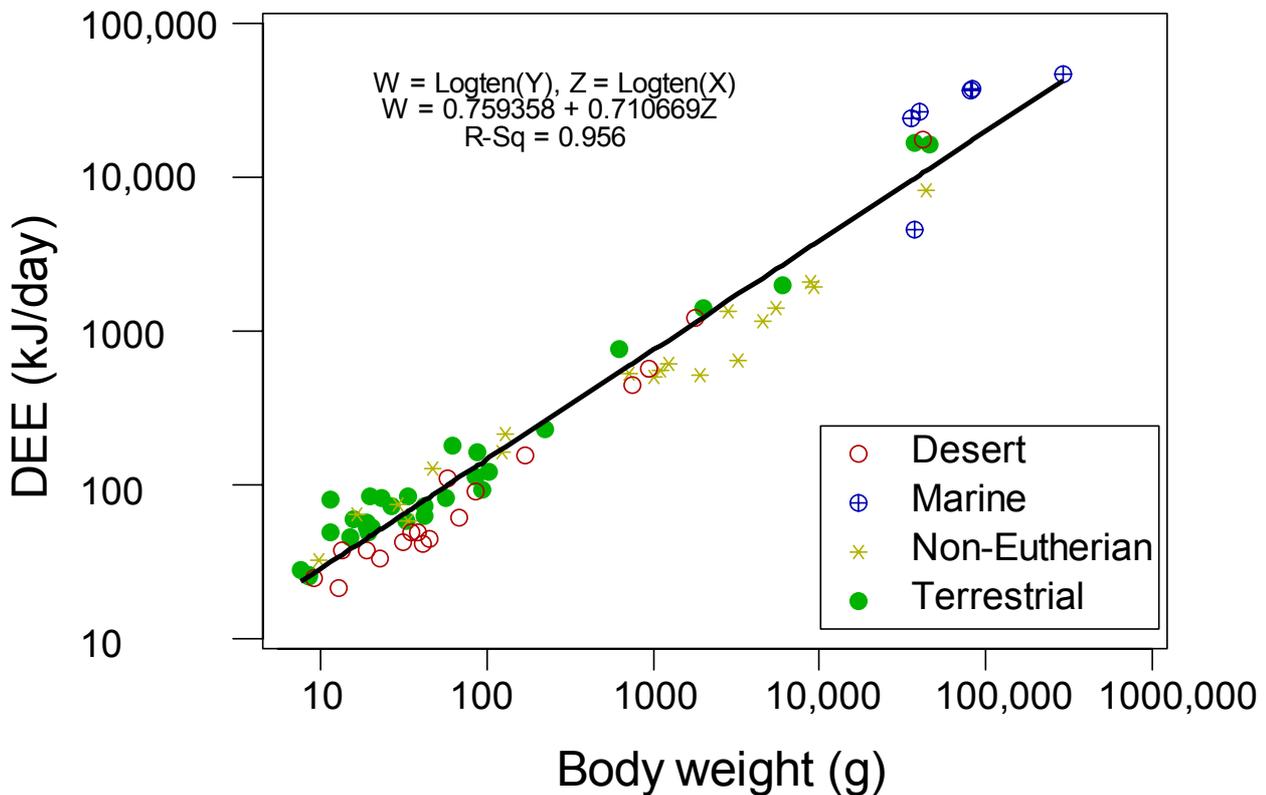


Figure 2. Relationship between log daily energy expenditure against log bodyweight for 73 mammal species



The equations estimate the DEE for any species from its mean bodyweight. The same equations might be used to predict the DEE of individual animals. For example, the equation might be used to predict not only the DEE of an average wood mouse but also of heavier and lighter wood mice. However, further analysis of our data on birds suggests that the relationship between body weight and DEE scales differently within a species than between species (Table 3). The same point has been argued by Tinbergen and Dietz (1994) who found that among breeding great tits, the slope linking small individuals with heavy individuals is close to 2, much steeper than the value of 0.7 we found linking light species with heavy species. In other words, it is energetically very costly to be an overweight great tit at least during the breeding season. The authors speculate that during this time great tits feeding young spend much time in hovering flight taking small caterpillars. This may be a proportionately more strenuous activity for heavier birds. Therefore the equations derived in this study use mean bodyweight for a species and do not attempt to model the effects of individual variation in bodyweight.

Within bird species, the breeding status of the individual had an important influence on DEE. As might be expected, birds feeding young used more energy than incubating birds (Table 3).

Table 3 Weighted least squares regression of DEE on body weight, species and breeding status based on data for individual birds or groups (where data for individuals were not listed).

Dependent Variable: Log DEE

Source	Type I Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	694.6	209	3.3	399.	<.001
Intercept	10299.1	1	10299.1	1236465	<.001
LOGBWT	641.8	1	641.8	77051	<.001
SPECIES	42.1	95	.4	53	<.001
BREEDSTATUS	4.0	4	1.0	119	<.001
SPECIES * LOGBWT	4.2	65	6.400E-02	8	<.001
SPECIES * BREEDSTATUS	2.0	29	6.899E-02	8	<.001
BREEDSTATUS * LOGBWT	.2	2	.1	12	<.001
SPECIES * BREEDSTATUS * LOGBWT	.4	13	3.301E-02	4	<.001
Error	4.8	579	8.329E-03		
Total	10998.6	789			
Corrected Total	699.5	788			

R Squared = .993 (Adjusted R Squared = .991)

Weighted Least Squares Regression - Weighted by Number of cases

Moisture and energy content of foods

Means for 15 major groupings of food types are presented in Table 4.

Table 4. Energy and moisture contents for 15 general categories of food type, based on a total of 1783 reported values for energy and 761 for moisture.

Food type	Energy content (Kj/g dry weight)	Moisture content (%)
Dicotyledenous crop leaves	11.2	88.6
Grasses and cereal shoots	18.0	76.4
Non-grass herbs	18.0	82.1
Tree leaves	20.7	51.4
Orchard topfruit	11.6	83.7
Cereal seeds	16.7	13.3
Weed seeds	21.0	11.9
Small mammals	21.7	68.6
Bird and mammal carrion	22.6	68.8
Arthropods	21.9	70.5
Caterpillars	21.7	79.4
Soil invertebrates	19.3	84.6
Fish	20.7	71.1
Aquatic invertebrates	19.6	77.3
Aquatic vegetation	15.0	81.4

Assimilation efficiency

The literature on avian digestive efficiency has been reviewed by Castro & Myers (1989), Karasov (1990) and most recently by Bairlein (1999). The latter author has collated data on more than 1000 examples of avian assimilation efficiencies reported in the literature and summarised them into 22 taxonomic groupings and six food types. We have relied mainly on Bairlein's summary for birds in this study. Data on assimilation efficiency of wild mammals is less common, but we have collected 91 examples. The main categories used in this study are listed in Table 5 (for mammals) and Table 6 (for birds).

Table 5. Assimilation efficiencies for mammals, based on 91 published examples.

Mammal group	Food type	Mean	n	Standard deviation
Shrews and bats	Insects	88	8	5.9
Carnivores	Vertebrates	85	16	5.8
Squirrels	Nuts	85	10	7.5
Small mammals	Nuts and seeds	83	11	8.5
Small mammals	Grasses	46	15	10.7
Small mammals	Crops, forbs, mixed vegetation	74	17	12.3
Lagomorphs	General vegetation	74	4	13.5
White tailed deer	Tree browse	32	7	8.4
Ruminants	Hay and browse	80	3	2.8

Table 6. Assimilation efficiencies for birds, from Bairlein (1999). N species = number of species, N cases = number of studies.

Order		N Species	N cases	Food type					
				animal	fruits	herbage	seeds	sugars	artificial
Struthioniformes	Ostriches	2	6				36		
Gruiformes	Cranes, coots, rails	1	5	34	45		59		69
Ralliformes	Coots, rails	1	1						
Charadriiformes	Gulls, waders	7	19	69					74
Lariformes	Gulls, terns	1	3	79					
Alciformes	Auks	1	2	76					
Sphenisciformes	Penguins	7	26	75					
Procellariiformes	Petrels	2	3	87					
Pelecaniformes	Pelicans, gannets, cormorants	4	8	80	76				
Columbiformes	Pigeons	4	36						76
Psittaciiformes	Parrots	1	4					96	
Strigiformes	Owls	6	45	77					
Falconiformes	Eagles, falcons	4	12	84					
Accipitriformes	Hawks	11	22	82					
Ciconiiformes	Hérons, storks	4	8	80					
Anseriformes	Ducks, geese	22	98	87		41	83		74
Galliformes	Fowl	18	184	70	57	42	65		67
Opisthocomiformes	Hoatzin (S. America)	1	2						74
Trochiliformes	Hummingbirds	7	16					98	
Coliiformes	Mousebirds (Africa)	4	15		56				73
Piciformes	Woodpeckers	1	14	64		61			80
Passeriformes	Passerines	67	441	76	67	76	80	90	72

Estimation of average daily food intake

Daily food intake was estimated for 82 scenarios of typical UK birds and mammals consuming typical foods that could potentially be contaminated with pesticides. In each case, the most relevant subset of the available information was used. DEE has not been measured directly for most of the species of concern in risk assessment. In these cases, we used the general equations in Table 1 (for birds) and Table 2 (for mammals) to estimate DEE. These estimate the mean DEE for a species from its mean bodyweight. It should be remembered that there is additional variation between species within the habitat groups, and there are also differences due to breeding status (at least for birds) and variation over time, but these sources of variation are not sufficiently well characterised by existing data to be included in general equations. Occasionally we had good direct measurements of DEE for individual species that might figure in agricultural pesticide risk assessments. Where possible we used these empirical data to calculate likely food intake.

Consider, for example, the weight of insects a chaffinch would need to eat in a day in order to maintain its energy budget. A chaffinch is a small passerine, therefore, using the appropriate equation from Table 1, ($\text{Log}_{10}(\text{DEE}) = 1.0017 + 0.7034 \times \text{log}_{10}(20.9)$), it might expect to expend 85.2 kJ per day. Arthropods contain an average of 21.9 kJ/g dry weight and consist of 70.5% water (Table 4). Therefore arthropods contain 6.5 kJ/g fresh weight. A bird using 85.2 kJ a day will need $85.2/6.5 = 13.2\text{g}$ of arthropods, assuming it can digest its food completely efficiently. However, studies suggest that on average, passerines only manage to make use of 76% of the energy in animal foods (Table 6). Therefore, on average a chaffinch balancing its daily energy budget and feeding wholly on arthropods will need to eat 17.3g fresh weight a day.

The results of similar calculations for all 82 scenarios are presented in Table 7 for birds and Table 8 for mammals.

Table 7. Predicted fresh food intake for selected combinations of UK bird species and food types.

Food	Species	Body Wt	Mean	
			food intake	
		(g)	(g)	
Aquatic invertebrates	Dipper	<i>Cinclus cinclus gularis</i>	101.0	88.7
	Mallard	<i>Anas platyrhynchos</i>	1082.0	280.4
Aquatic vegetation	Mallard	<i>Anas platyrhynchos</i>	1082.0	846.0
Arthropods	Chaffinch	<i>Fringilla coelebs</i>	20.9	17.3
	Corn bunting	<i>Miliaria calandra</i>	43.9	29.2
	Goldcrest	<i>Regulus regulus</i>	5.7	7.0
	Great spotted woodpecker	<i>Dendrocopus major</i>	81.6	28.3
	Grey partridge	<i>Perdix perdix</i>	381.0	97.6
	Lapwing	<i>Vanellus vanellus</i>	211.0	98.3
	Nuthatch	<i>Sitta europaea</i>	22.0	18.0
	Pheasant	<i>Phasianus colchicus</i>	953.0	198.1
	Rook	<i>Corvus frugeligus</i>	488.0	159.1
	Skylark	<i>Alauda arvensis</i>	37.2	26.0
	Starling*	<i>Sturnus vulgaris</i>	79.8	50.9
	Tree sparrow	<i>Passer montanus</i>	22.0	18.0
	Wren	<i>Troglodytes troglodytes</i>	8.9	9.5
	Yellowhammer	<i>Emberiza citrinella</i>	26.5	20.5
Birds	Sparrowhawk	<i>Accipiter nisus</i>	149.0	42.2
Bugs	Blue tit*	<i>Parus caeruleus</i>	11.5	13.5
Carrion	Buzzard	<i>Buteo buteo</i>	781.0	137.7
	Crow	<i>Corvus corone corone</i>	570.0	162.2
Caterpillars	Blue tit*	<i>Parus caeruleus</i>	11.5	18.9
Cereal seeds	Corn bunting	<i>Miliaria calandra</i>	43.9	12.4
	Grey partridge	<i>Perdix perdix</i>	381.0	50.6
	Pheasant	<i>Phasianus colchicus</i>	953.0	102.7
	Rook	<i>Corvus frugeligus</i>	488.0	67.5
	Tree sparrow	<i>Passer montanus</i>	22.0	7.6
	Woodpigeon	<i>Columba palumbus</i>	490.0	53.1
	Yellowhammer	<i>Emberiza citrinella</i>	26.5	8.7
Dicot crop leaves	Skylark	<i>Alauda arvensis</i>	37.2	224.8
	Woodpigeon	<i>Columba palumbus</i>	490.0	999.8
Earthworms	Blackbird	<i>Turdus merula</i>	113.0	119.5
	Buzzard	<i>Buteo buteo</i>	781.0	316.8
	Lapwing	<i>Vanellus vanellus</i>	211.0	141.4
	Starling*	<i>Sturnus vulgaris</i>	79.8	107.1

* denotes species for which a published measurement of DEE was used instead of an estimate from the equations in Table 1 and Table 2.

Table 7 (continued). Predicted fresh food intake for selected combinations of UK bird species and food types.

Food	Species	Body Wt	Mean	
			food intake	
		(g)	(g)	
Fish	Goosander*	<i>Mergus merganser</i>	1417.0	418.4
	Heron	<i>Ardea cinerea</i>	1443.0	274.2
	Kingfisher	<i>Alcedo atthis</i>	27.0	13.1
Fruit buds	Bullfinch	<i>Pyrrhula pyrrhula</i>	21.8	66.5
Monocot leaves	Canada Goose	<i>Branta canadensis</i>	3314.0	1426.8
	Greylag Goose	<i>Anser anser</i>	3108.0	1357.8
	Mallard	<i>Anas platyrhynchos</i>	1082.0	601.1
Oilseed rape grain	Linnet	<i>Carduelis cannabina</i>	15.3	4.9
Slugs & snails	Lapwing	<i>Vanellus vanellus</i>	211.0	145.5
	Song thrush	<i>Turdus philomelos</i>	66.6	84.8
Small mammals	Barn Owl	<i>Tyto alba</i>	294.0	72.9
	Kestrel*	<i>Falco tinnunculus</i>	209.0	78.7
	Little owl	<i>Athene noctua</i>	164.0	46.4
	Tawny Owl	<i>Strix aluco</i>	426.0	97.1
Top fruit	Blackbird	<i>Turdus merula</i>	113.0	221.4
	Song thrush	<i>Turdus philomelos</i>	66.6	152.6
Tree seeds	Great spotted woodpecker	<i>Dendrocopus major</i>	81.6	8.8
	Nuthatch	<i>Sitta europaea</i>	22.0	5.4
Weed seeds	Chaffinch	<i>Fringilla coelebs</i>	20.9	5.8
	Goldfinch	<i>Carduelis carduelis</i>	15.6	4.7
	Linnet	<i>Carduelis cannabina</i>	15.3	4.6

* denotes species for which a published measurement of DEE was used instead of an estimate from the equations in Table 1 and Table 2..

Table 8. Predicted fresh food intake for selected combinations of UK mammal species and food types.

Food	Name	Species	Body Wt	Mean food intake
			(g)	(g)
Arthropods	Badger	<i>Meles meles</i>	10100.0	851.7
Arthropods	Common shrew*	<i>Sorex araneus</i>	12.0	12.8
Arthropods	Fox	<i>Vulpes vulpes</i>	5700.0	569.0
Arthropods	Harvest mouse	<i>Micromys minutus</i>	7.0	4.9
Arthropods	Hedgehog	<i>Erinacus europaeus</i>	1100.0	173.1
Arthropods	Pipistrelle*	<i>Pipistrellus pipistrellus</i>	7.6	5.2
Arthropods	Wood mouse*	<i>Apodemus sylvaticus</i>	20.5	12.0
Aquatic invertebrates	Water shrew	<i>Neomys fodiens</i>	15.0	12.4
Cereal seeds	Harvest mouse	<i>Micromys minutus</i>	7.0	2.3
Cereal seeds	Wood mouse*	<i>Apodemus sylvaticus</i>	20.5	5.7
Nuts	Red squirrel	<i>Sciurus vulgaris</i>	300.0	22.7
Grass, Cereal shoots	Fallow deer	<i>Dama dama</i>	44000.0	3798.6
Grass, Cereal shoots	Rabbit	<i>Oryctolagus cunicula</i>	1500.0	390.9
Grasses	Field vole*	<i>Microtus agrestis</i>	26.5	37.7
Forbs	Field vole*	<i>Microtus agrestis</i>	26.5	30.6
Browse	Muntjac	<i>Muntiacus reevesi</i>	12200.0	834.1
Aquatic vegetation	Water vole	<i>Arvicola terrestris</i>	272.0	162.7
Birds & Mammals	Fox	<i>Vulpes vulpes</i>	5700.0	520.2
Fish	Otter	<i>Lutra lutra</i>	7000.0	983.2
Small mammals	Polecat	<i>Mustela putorius</i>	689.0	130.9
Small mammals	Stoat	<i>Mustela erminea</i>	205.0	55.7
Small mammals	Weasel	<i>Mustela nivalis</i>	63.0	24.7
Worms & slugs	Badger	<i>Meles meles</i>	10100.0	1842.3
Earthworms	Common shrew*	<i>Sorex araneus</i>	12.0	27.8
Worms & slugs	Hedgehog	<i>Erinacus europaeus</i>	1100.0	374.4
Worms & slugs	Mole	<i>Talpa europea</i>	85.0	64.2

* denotes species for which a published measurement of DEE was used instead of an estimate from the equations in Table 1 and Table 2..

Discussion

The method presented here allows one to predict a species' likely consumption of a given diet from its bodyweight. The results are broadly in line with empirical data (Table 9 and Figure 3) and with EPPO's rule of thumb. Gibb (1957) fed coal tits (bodyweight 8.4g) freshly caught insects in an outdoor aviary and reported an average consumption of 8.13g a day. According to the EPPO rule of thumb they would be expected to eat 8.54 g, whereas the equation based on DLW studies suggests a daily consumption of 8.55g. Discrepancies between the DLW predictions and the EPPO rule of thumb are most obvious where bodyweight is near 100 g, because this is where the EPPO rule arbitrarily changes from an estimate based on 30% to one based on 10% of body weight.

Unlike a rule of thumb, the use of empirically derived equations allows us to estimate confidence limits on our predictions and they open up the possibility of predicting not only the most likely food intake but also the unlikely or worst case scenarios as well. Risk assessment is rarely concerned about the average outcome. For example, a risk policy that aimed to protect the average member of a population from unacceptable danger would, by definition, allow 50% of the population to be exposed to greater than acceptable risk. Therefore, risk managers try to consider the worst or "reasonable" worst case. If conditions are acceptable for the worst-case scenario then they should also be acceptable for the rest of the population.

Because we are able to characterise reasonably well the distribution of energy expenditure of wildlife, their assimilation efficiencies, and the energy and moisture contents of wildlife foods, then, as well as average food intake, we can also predict what worst case food intakes (eg 95th percentiles) for a species of a given size are likely to be. Our preliminary Monte Carlo simulations (using @Risk software, 1996) indicate that the 95% quantile for food intake was about twice the average intake. This suggests that a safety factor of about 2 might be appropriate in estimating a species' worst case food intake from data based on a mean intake. (Ideally we would like to be able to predict worst case intake for individuals within a population but this would require data linking DEE to individual bodyweights.)

Limitations in using theoretical models of food intake

Appropriateness of data on food quality

1. We have imperfect information about the composition of wildlife diets. We may be aware that a species is a grazer but may not know on what exactly it grazes and how this varies between individuals, season and habitat. Does blackbird in an orchard, eat the same things as a blackbird in a wood?
2. Our data reflect information on foods that are available in the literature rather than foods present in diets. We have therefore been obliged to categorise food types into broad categories (e.g. arthropods, seeds, leaves) under the assumption that food quality does not differ markedly within a category. It follows, nevertheless, that the values included may lean toward those that were reasonably easy to collect rather than those that best reflect what a particular animal might actually eat. Juvenile hobbies (*Falco subbuteo*) for example, are known to specialise on dragonflies (Clarke et al, 1996). Rather

than use the general mean for arthropod prey, it may be more appropriate in this case to select only values for *Odonata*.

3. The food items collected and measured by an experimenter may not match those selected by wildlife species. For example, the experimenter might take a sweepnet (e.g. Robel et al, 1995) to collect insects living in the favourite foraging habitat of a focal animal and measure their energy and moisture contents. Unfortunately a sweepnet is not a foraging bird (see Wolda, 1990; Hutto, 1990). There is much evidence that animals are seldom passive in their feeding behaviour and foods are rarely eaten in true proportion to their availability. Rather animals select some food items and reject others.
4. Food is not only a source of energy. We have estimated daily food intake of wild animals by dividing the energy requirement of the animal by the energy provided in the food. However, food contains many other valuable constituents, such as protein, minerals and vitamins. Animals may be feeding in order to satisfy their need for protein (e.g. for nestlings) rather than balancing a simple energy budget. They may make trade-offs between competing goals.

Appropriateness of data on Daily Energy Expenditure

1. Variance in DEE is high. Although the equations linking bodyweight with DEE (Table 1 and Table 2) often explain 90% or more of the variance, the correlation is based on log bodyweight against log DEE. Small variations along a log scale translate to large differences on the untransformed data. Thus although we can say that on average a 20g wood mouse will use 47kJ of energy a day, the lower and upper 95% confidence limits are 22 and 102kJ a day.
2. DEE may be overestimated. The majority of DLW studies on birds have taken place when birds are nesting and it is easier to catch them repeatedly. For non-tropical birds, the breeding season is likely to be a time when the days are long, and birds are particularly busy gathering food for their young. Their DEE at other times may be significantly less (see Table 3).
3. Animals may choose to expend less energy rather than seek more food. We should not assume that energy expenditure is a fixed requirement beyond the control of the animal. An individual facing food shortages may choose to conserve energy rather than search for new sources. If searching is itself an expensive activity, animals may prefer to sit tight until the situation improves. This, in essence, is what hibernating animals do. McDevitt and Speakman (1994) found that when field voles were exposed to low temperatures for short periods they did not respond, as the authors expected, by increasing food intake. Rather they decreased foraging activity, preferring to stay relatively warm in their nests than venture into a cold environment in search of food. Similarly, sugar beet leaves may be a low quality food for an active skylark but for a bird feeding quietly in a beet field, their super-abundance and hence the small amount of energy spent finding them, may make up for their poor quality. This may explain why skylarks have achieved pest status in sugarbeet fields (Green, 1980) and woodpigeons in oilseed rape (Inglis et al, 1990).
4. Animals may choose not to balance their energy budgets. A key assumption in using DEE to predict food consumption is that animals on average must find enough food to supply their daily energy needs. In the long term this must be true. In the short term however, they may choose to make use of fat reserves,

losing bodyweight, rather than wasting effort foraging on inadequate food sources. In other contexts winter passerines appear to trade bodyweight for reduced predation risk even though the risk of starvation is thereby increased (Brodin, 2001).

Plausibility of food intake predictions.

We have already noted that in most cases the food intake values predicted by our model are in broad agreement with empirical data and with the EPPO rule of thumb. However, there are examples, particularly for small animals feeding largely on leaves where the predicted daily food intakes seem unreasonably large. For example, the model implies that a skylark weighing 37g will eat 225g of beet leaves a day – more than 6 times its own bodyweight. This seems unlikely. However, the model does not imply that a skylark *will* eat 6 times its own bodyweight each day in beet leaves, rather it stating that this is what a skylark would need to eat if it ate nothing but beet leaves and was obliged to balance its energy budget.

If it seems unlikely that a skylark could eat 6 times its own bodyweight in a day, we should ask what a likely maximum food intake would be. Table 9 contains examples of empirical attempts to estimate food intake of wild birds or birds held in captivity under realistic conditions. The most voracious eater would appear to be the rufous-tailed plantcutter, a passerine weighing 40g which in captivity ate more than 5 times its own bodyweight in lettuce leaves every day (Lopez-Calleja & Bozinovic (1999)). In practice however, skylarks take a mixed diet (Donald et al 2001) and it would not be common to feed wholly on leaves. Where the diet of an animal normally consists of a range of foods then the risk assessment should reflect this, estimating food intake when several different foods are consumed in known proportions.

For example, Donald et al (2001) found that the diet of skylarks on winter cereal fields comprised 54% cereal leaves (16kJ/g, 85% moisture, 45% assimilation) and 24% weed leaves (18kJ/g, 82% moisture, 45% assimilation) 13% cereal grain (17.3kJ/g, 13.7% moisture, 80% assimilation), 5% weed seeds (20.9kJ/g, 11.9% moisture, 80% assimilation) and 3% arthropods (21.9kJ/g, 70.5% moisture, 76% assimilation). Using Donald et al's data on dietary proportions and our own data on nutrient values and assimilation efficiencies we can show that a daily energy budget of 128kJ for a 37g skylark could be satisfied by eating 20.4g cereal leaves, 9.1g broadleaf weeds, 4.9g grain, 1.9g of weed seeds, and 1.1g arthropods: in all a daily food intake of 37.5g.

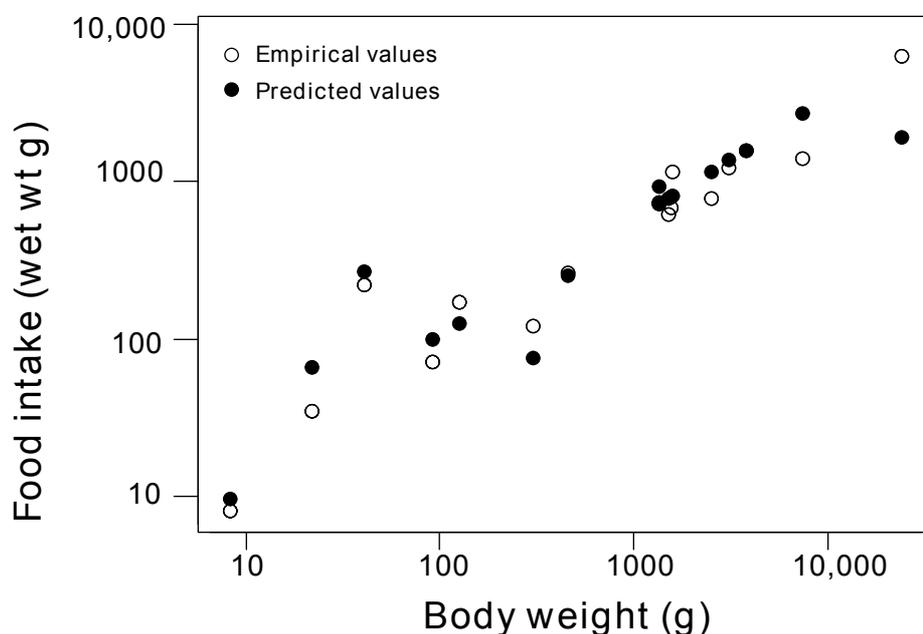
Table 9. Examples of food intake estimated for wild birds or high food intake measured for captive birds

Species	Food	Body Wt (g)	Food Intake (g)	% of Body Wt	Reference	Comment
Coal tit	Insects	8.4	8.13	96.8	Gibb (1957)	Kept in outdoor aviary in mid October (temp = 13.7) fed a diet of freshly killed mixed insects (40% caterpillars, 25% spiders) with moisture content of 70.5%.
Bullfinch	Pear buds	22	35	159	Summers (1982)	Kept in outdoor aviaries in winter and fed on pear tree prunings.
Cedar waxwings	Artificial / fruit	37	55.9	151	McWilliams et al 1999	Kept in captivity at -20°C.
Rufous-tailed Plantcutter	Lettuce	40.5	219	540	Lopez-Calleja & Bozinovic (1999)	Kept in captivity on a diet of lettuce for 6 days.
Blackbirds	Earthworms	91	71	78	Fryday 1996 (unpublished)	Kept in outdoor aviaries in October and feeding time restricted to 6 hours a day on fresh juvenile <i>Lumbricus terrestris</i> . All birds lost weight during the trial.
Woodcock	Earthworms	126	169	134	Stickel (1965)	Captive birds, kept on ¼ rations for 10 days lost approximately 20% initial body weight. When allowed unrestricted feeding for 5 days weight was mostly regained. Maximum consumption reached 230 g.
Barn Owl	Mice	305	120	39	Handrich et al (1993)	Kept at 5°C and starved, losing 30% of body weight. Maximum consumption by a 305 g female which ate 4 mice
Oystercatcher	Shellfish	460	261.8	57	Hulscher (1974)	Captive birds ate an average of 154 g of Cockles and Mussels (<i>Cardium</i> and <i>Mytilus</i>). From field observations he estimates that wild birds in summer might eat 1.4 times as much and in winter 1.7 times
Brent goose	Eel grass (Zostera)	1350	717	53	Percival & Evans (1997)	Based on faeces production of birds feeding in inter-tidal zone. Birds consumed 132 g dry matter a day. Estimate assumes 82% moisture.
Brent goose	Grass	1350	749	55	Boudewijn (1984)	Based on faeces production of wild birds in winter. Data originating from Drent (1978). Geese ate 175 g dry matter a day. Estimate assumes moisture content of 77%.
Brent goose	Grass	1600	1156	72	Boudewijn (1984)	Based on faeces production of wild birds in spring. Data originating from Drent (1978). Geese ate 270 g dry matter a day. Estimate assumes moisture content of 77%.

Table 9. Continued

Species	Food	Body Wt (g)	Food Intake (g)	% of Body Wt	Reference	Comment
Ruddy-headed goose	Grass	1500	620	41	Summers & Grieve (1982)	Based on faeces production of wild birds. Estimated gross intake 2600 kJ. Assuming 4.2 kJ/g , geese were consuming 620 g wet wt of grass a day.
Barnacle goose	Grass	1550	676	39	Ebbinge et al (1975)	Based on faeces production on pasture. Geese produce 106 g dry wt of droppings each day, and given 33% retention of food eaten, therefore consume 158 g dry wt of grass. Given 77% moisture content, geese consume 676 g wet wt of grass. Authors estimate a maximum intake ceiling of 1091 –1446 g
Pink footed goose	Grass	2500	770	28	Madsen (1985)	Based on faeces production on pasture. Geese produce 132 g dry wt of droppings each day, and given 26.7% retention of food eaten, they therefore consume 180 g dry wt of grass. Given 77% moisture content, geese consume 690 g wet wt of grass.
Uplands goose	Grass	3100	1241	40	Summers & Grieve (1982)	Based on faeces production of wild females in summer. Estimated gross intake 5200 kJ. Assuming 4.2 kJ/g , geese were consuming 1241 g wet wt of grass a day.
Uplands goose	Grass	3800	1599	42	Summers & Grieve (1982)	Based on faeces production of wild females in summer. Estimated gross intake 6700 kJ. Assuming 4.2 kJ/g , geese were consuming 1599 g wet wt of grass a day.
Domesticated (Landes) Goose	Artificial diet	7400	1413	19	Auffray & Marcilloux (1980)	Hyperphagic after hypothalamic lesion. Fed semi liquid diet comprising 1 part meal, 2 parts water.
Emperor penguin	Fish	24200	6300	26	Robertson & Newgrain 1996	Feeding young. Food intake trebled from 2.3 kg a day in winter when chicks weighed < 5% adult mass to (adults weighed 26 kg) to 6.3 kg a day when chicks were 40-50% of adult mass of 24.2 kg.

Figure 3. Empirical values for wildlife food intake as measured directly (Table 9) compared with predicted intake based on DEE.



Implications for risk assessment

The equations for average daily food intake derived in this study are intended for use in the risk assessment of pesticides and other contaminants. Estimates for 82 scenarios may be read directly from Table 7 and Table 8. Estimates for other combinations of species and foods may be obtained by using the equation 1, the equations for DEE in Table 1 and Table 2, and relevant estimates of food energy content, moisture content and assimilation efficiency from Table 4 to Table 6.

The equations and estimates presented here are based on the data reviewed for this report. If the user has data on DEE, energy content, moisture content, or assimilation efficiency, which are more relevant to the assessment scenario, these data should be used to replace the corresponding approximation in the standard equations.

If the user has reliable information on dietary composition for the species of interest, this may be used to refine the estimate of intake. In doing this it is important to take account of the units of the data on dietary composition. In general dietary composition will be reported as proportions in terms of mass, volume or number of items rather than energy. As the energy contents of different foods vary, a slightly more complex calculation using simultaneous equations is required to estimate the amounts of each food type needed to satisfy both the energy requirement and the observed dietary composition. (See the example for skylark above.)

The user should bear in mind that the estimates of food intake are uncertain because of the limitations of the underlying data and the need to extrapolate DEE and assimilation efficiency between species. The true average daily intake could be significantly higher or lower than the estimate. Preliminary probabilistic analysis

indicated that the upper 95th percentile for the estimate averaged about twice the mean estimate. This result is preliminary, but indicates the potential range of uncertainty. If the user wished to be precautionary in their assessment, multiplying the estimated food intake by a factor of two might be a reasonable precaution against underestimating food intake. However, it would be preferable to obtain definitive confidence limits from a more refined probabilistic analysis.

The user should also bear in mind that for any species, daily food intakes vary between individuals. Part of this variation is due to the influence of breeding status: birds feeding young were shown to use more energy than other individuals (Table 1). Also, for the same individual, intake will vary from day to day. Ideally these sources of variation should be taken into account in risk assessment, but to do this would require further development.

In many or most assessments, the estimates provided by this study will be sufficient. However, if the result of a risk assessment is close to a regulatory threshold then the assessor may need to refine the assessment in order to reach a decision. In such cases, consideration could be given to refining the estimate of food intake. Possible options might include obtaining measurements of energy and moisture content for relevant foods sampled in relevant conditions. These could then be substituted in the equations from this study. If necessary, consideration could be given to measuring assimilation efficiencies for relevant species and foods, or even measuring DEE for relevant species in relevant conditions. (Of course, there are other elements of the risk calculation that might also benefit from further refinement e.g. residue levels of food items.)

Whether or not new data are obtained, food intake will still vary (e.g. between individuals) and some uncertainties will remain. A refined assessment may therefore need to use probabilistic methods to examine the influence of variation and uncertainty on risk (e.g. to estimate what proportion of a population will be affected). It may be helpful to carry out a probabilistic assessment before requesting costly new data (e.g. measurements of DEE or assimilation efficiencies), to evaluate their likely influence on the assessment outcome.

Acknowledgements

This work was funded by the Department for Environment, Food and Rural Affairs.

References

- @Risk (1996) Risk analysis and simulation add-in for Microsoft Excel or Lotus 1-2-3. Palisade Corporation, New York.
- Auffray, F.P. & Marcilloux, J.C. (1980) Effect of induced hypothalamic hyperphagia and forced feeding on organ weight and tissular development in Landes geese. *Reprod.Nutr.Develop.*, **20**, 709-717.
- Bairlein, F. (1999) Energy and nutrient utilization efficiencies in birds - a review. In Adams, N. and Slotow, R. (Eds.) *Proceedings of the 22nd International Ornithological Congress, Durban Birdlife South Africa*

- Brodin (2001) Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation? *Animal Behaviour* **62**: 993-999.
- Boudewijn, T. (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl*, **35**, 97-105.
- Castro, G., Myers, J.P., & Ricklefs, R.E. (1992) Ecology and energetics of sanderlings migrating to 4 latitudes. *Ecology*, **73**, 833-844.
- Clarke, A., Prince, P.A., & Clarke, R. (1996) The energy content of dragonflies (*Odonata*) in relation to predation by falcons. *Bird Study*, **43**, 300-304.
- Ebbinge, B., Canters, K., & Drent, R. (1975) Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl*, **20**, 5-19.
- EPPO/CoE (1994) Decision-making scheme for the environmental risk assessment of plant protection products. *EPPO bulletin*, **24**, 37-87.
- Gibb, J. (1957) Food requirements and other observations on captive tits. *Bird Study*, **4**, 207-215.
- Green, R.E. (1980) Food selection by skylarks and grazing damage to sugar beet seedlings. *Journal of Applied Ecology*. **17**:613-630.
- Handrich, Y., Nicolas, L., & Le Maho, Y. (1993) Winter starvation in captive common barn-owls: bioenergetics during re-feeding. *Auk*, **110**, 470-480.
- Hulscher, J.B. (1974) An experimental study of the food intake of the oystercatcher *Haematopus ostralegus* L. in captivity during the summer. *Ardea*, **62**, 156-171.
- Hutto, R.L. (1990) Measuring the availability of food resources. In Morrison, M. L., Ralph, C. J., Verner, J., and Jehl, J. R. (Eds.) *Avian foraging: theory, methodology, and applications*, pp. 20-28., San Diego
- Inglis, I.R, Isaacson, A.J.R., Thearle J. P, and Westwood N. J. (1990) The effects of changing agricultural practice upon woodpigeon *Columba palumbus* numbers. *Ibis* **132** (2):262-272.
- Karasov, W.H. (1990) Digestion in birds: chemical and physiological determinants and ecological implications. In Morrison, M. L., Ralph, C. J., Verner, J., and Jehl, J. R. (Eds.) *Avian foraging theory, methodology and applications*, pp. 391-415. Cooper Ornithological Society
- Nagy, K.A. (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*, **57**, 111-128.
- Nagy, K.A., Girard, I.A. and Brown, T.K. (1999) Energetics of free-ranging mammals, reptiles and birds. *Annual Review of Nutrition*, **19**, 247-277.

- Lopez-Calleja, M.V. & Bozinovic, F. (1999) Feeding behaviour and assimilation efficiency of rufous-tailed plantcutter. *Condor*, **101**, 705-710.
- Madsen, J. (1985) Relations between change in spring habitat selection and daily energetics of Pink-footed geese, *Anser brachyhynchus*. *Ornis Scandinavica*, **16**, 222-228.
- Mcdevitt, R. & Speakman, J.R. (1999) Limits to sustainable metabolic rate during transient exposure to low temperatures in short-tailed field voles (*Microtus agrestis*). *Physiological Zoology*, **67**, 1103-1116.
- McWilliams, S.R., Caviedes-Vidal, E., & Karasov, W.H. (1999) Digestive adjustments in cedar waxwings to high feeding rate. *Journal of Experimental Zoology*, **283**, 394-407.
- Percival, S.M. & Evans, P.R. (1997) Brent Geese *Branta bernicla* and *Zostera*; Factors affecting the exploitation of a seasonally declining food resource. *Ibis*, **139**, 121-128.
- Robel, R.J., Henning, B.L., Johnson, K.W., Blocker, H.D., & Kemp, K.E. (1995) Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology*, **66**, 44-53.
- Robertson, G. & Newgrain, K. (1996) The food and energy intake rates of adult emperor penguins (*Aptenodytes forsteri*) rearing chicks. *Antarctic Science*, **8**, 37-44.
- Stickel, W.H., Hayne, D.W., & Stickel, L.F. (1965) Effect of heptachlor-contaminated earthworms on woodcocks. *Journal of Wildlife Management*, **29**, 132-146.
- Summers, D.B.B. (1982) The survival of bullfinches on cultivated fruit buds. *Journal of Applied Ecology*, **19**, 813-819.
- Summers, R.W. & Grieve, A. (1982) Diet, feeding behaviour and food intake of the upland goose (*Chloephaga picat*) and ruddy-headed goose (*C. Chloephaga picat. rubidiceps*) in the Falkland Islands. *Journal of Applied Ecology*, **19**, 783-804.
- Tinbergen, J.M. & Dietz, M.W. (1994) Parental energy-expenditure during brood rearing in the great tit (*parus-major*) in relation to body-mass, temperature, food availability and clutch size. *Functional Ecology*, **8**, 563-572.
- Wolda, H. (1990) Food availability to an insectivore and how to measure it. In Morrison, M. L., Ralph, C. J., Verner, J., and Jehl, J. R. (Eds.) *Avian foraging: theory, methodology, and applications*, pp. 38-43. Cooper Ornithological Society, San Diego