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PROJECT I

Using ^{13}C and ^{14}N stable isotope analysis of egg tissue to indicate feeding from isotopically distinct dietary sources in a wild population of great skuas

PROJECT II & POSTER

Activity budget and feeding behaviour of the North American porcupine *Erethizon dorsatum*, in the Parc du Bic, Quebec, Canada

REVIEW ESSAY I

The population dynamics of red and grey squirrels in Britain

REVIEW ESSAY II

Review the underlying causes and potential solutions to the current conflict between agriculture and conservation in the management of goose populations in Scotland

Using ^{13}C and ^{14}N stable isotope analysis of egg tissue to indicate feeding from isotopically distinct dietary sources in a wild population of great skuas

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Abstract

The measurement of stable isotopes of carbon and nitrogen in tissue can offer dietary information about freshwater and marine dietary sources, and the trophic level of feeding in seabirds. The isotope signature of a tissue reflects the assimilated constituents of the diet and may reflect short-, medium- and long-term diet, depending upon the tissue analysed. Because the components of eggs are ultimately derived from the diet of the female bird, the isotopic signature of the egg tissue might be expected to be related to the diet. Wild great skuas *Catharacta skua* were fed a catfood dietary supplement (representing a terrestrial, primary consumer food source), and their eggs were isotopically analysed and compared to wild-feeding birds assumed to be consuming a sandeel diet *Ammodytes marinus* (representing a marine, secondary consumer). The eggs of both groups of birds reflected their respective diets. A significant difference was observed between fed and unfed skua eggs. Fed birds eggs were depleted in ^{15}N by 1 $^{0}/_{00}$, and ^{13}C by – 0.9 $^{0}/_{00}$ compared to the unfed birds eggs. There was no evidence of a sequential trend in isotope signature within individual bird's clutches. Using isotope signatures of fed and unfed birds' eggs and estimates of projected 100 % catfood and sandeel contributions, the percentage contribution of catfood to the fed birds' diet was calculated at 12 %. The FMR (field metabolic rate) of a pair of adult breeding skuas was calculated at 3766 kJ, and the potential calorific contribution of the catfood diet to the fed pair was estimated at 29 %. This study suggests that egg tissue may be used to determine the diet of wild skuas that have been recently feeding on isotopically distinct diets, although the precise processes of nutrient transfer from diet to egg require further definition.

Acknowledgements

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Contents

1 Introduction

1.1 Avian nutrition and resource allocation relating to egg production

Nutrients necessary for maintenance, growth and repair include macronutrients of water, protein, lipid and carbohydrates, and micronutrients of vitamins and minerals. Proteins are of considerable importance, as their amino acid composition constitute the 'building blocks' necessary for the synthesis of body tissues. Any source of dietary protein must be sufficient to supply the required level of essential and non-essential amino acids (Klasing, 1998). Dietary proteins are consumed and catabolised to their amino acid molecules, which are further anabolised into tissues or used in intermediary metabolism. Tissues are in a state of continuous turnover, and excess amino acids that cannot be stored in the body are broken down to provide energy.

Dietary requirements of birds (and other species) vary with the energetic demands facing the individual. Egg production and growth are considered the most nutritionally demanding periods of an adult bird's life. During egg production, amino acids are required for the processes of oviduct development and egg protein deposition, in addition to normal body maintenance (Klasing, 1998). Egg albumen is composed of ~ 12% protein and ~ 25% yolk (Carey, 1996). Therefore, it may be reasonable to speculate that birds may require a source of amino acids additional to dietary proteins to enable them to produce quality eggs.

Although most nutrients deposited in (hen) eggs originate from the diet (Carey, 1996), it has been demonstrated in many species that body tissue is mobilised to supply the necessary amino acids during reproductively demanding periods (Klasing, 1998). For example, pectoral muscle and other tissues may be used as a source of protein for egg production in zebra finches, *Poephila guttata* (Selman & Houston, 1996; Houston *et al.*, 1995a, 1995b). Three possible scenarios have been proposed relating to the source of the nutrients required for egg production (which may not be exclusively separate): 1) Birds may increase their intake due to increasing nutrient demands; 2) Birds may not be able to take in adequate levels of protein to satisfy demands for egg formation in addition to their own basic metabolic requirements, hence there may be some mechanism to 'divert ' the protein directly

from diet to developing egg; 3) Birds may use their own protein store (muscle may serve to act as such a store), and proteins from this source may be then mobilised as an egg protein reserve (Jones & Ward, 1976; Kendall *et al.*, 1973; Houston *et al.*, 1995a, 1995b).

The complexities surrounding tissue-egg resource allocation in a wild bird population have received little attention. In considering whether the protein of birds' egg has a direct dietary source, or whether it originates from amino acids incorporated first as body tissue, stable isotopes may provide the necessary means to explore resource allocation in a wild bird population.

1.2 Stable isotopes - introduction and application

1.2.1 Isotope definition

Atoms vary slightly in their mass number and atomic number by the number of neutrons they possess. Nuclides of the same element of different atomic mass are called isotopes of that element. Every element has a number of different isotopes occurring naturally in nature, usually existing as two or more distinct stable isotopes (Criss, 1999). For example carbon exists as two stable isotopes of mass numbers 12 and 13, with a relative abundance of 98.9% and 1.10% respectively. Nitrogen exists as isotopes of mass 14 and 15, with abundance of 99.634% and 0.366% (Platzner, 1997). The atomic weights and relative abundance of nuclides from a particular sample can be determined using a mass spectrometer, and the proportion of isotope in any sample may be expressed in the delta (δ) notation of parts per thousand (see Methods for fuller explanation).

1.2.2 Isotopic fractionation

Fractionation of isotopes describes a change in isotope ratio of a substance. A sample may become partitioned into two or more isotope 'fractions' that subsequently have a ratio of 'heavy': 'light' isotopes, different to that of the initial naturally occurring (geochemical) ratio. Following isotopic analysis if there is found a greater representation of the heavy isotopes than the starting ratio, the sample is considered isotopically enriched through such fractionation processes. Conversely, if

there is a lower proportion of heavier isotopes then the sample is classified as isotopically depleted (Criss, 1999).

1.2.3 Stable isotopes as ecological tools

The process of fractionation occurs in biological processes such as the anabolism and catabolism of tissue. Early isotope studies identify carbon and nitrogen isotopes of animal tissues and organs from animals fed diets of known isotopic value to be slightly enriched relative to their diets (Deniro and Epstein, 1978, 1980). As the biochemical fractions of the diet are incorporated into animal tissue they become slightly isotopically altered. However the resulting isotopic composition of animal tissue still relates to that of the diet (Deniro and Epstein, 1978, 1980; Tieszen & Boutton, 1983; Hobson, 1999; Kelly, 2000). It is this feature of isotope expression that makes it a valuable ecological tool.

The technique of using stable isotope ratios to identify and predict diet in animals is becoming increasingly widely used (Kelly, 2000). Traditional diet studies have relied on either direct feeding observations or attempting to identify partially digested stomach contents or faeces. Such methods are tedious and often biased (Kelly, 2000). Reliable feeding observation data are difficult to obtain for seabirds as the birds may range far out to sea whilst foraging. The advantage of using isotopes are threefold: 1) isotopes can be measured quantitatively using precise spectrometric methods; 2) isotopes may represent a history of assimilated dietary input over several weeks or months as the isotopes ingested are metabolised at different rates in different tissue components (Tieszen & Boutton, 1983); 3) there is the potential for non-destructive sampling when using isotopes (Hobson & Clark, 1993). The use of stable isotopes in dietary analysis is of particular value where a consumer is utilising two isotopically distinct dietary sources, whereby it is possible to assess the relative dependence of the consumer on each food source.

1.2.3.1 Nitrogen

The most common approach to foodweb studies is to reconstruct the web interactions based on known feeding strategies (Schoeninger & DeNiro, 1984). Isotopes may be used to simplify this process and reduce the time-consuming process of categorising food web members in this way. This is possible because nitrogen isotope differences

may be used to identify trophic interactions in ecological systems. The heavier ^{15}N isotope is preferentially incorporated into tissues of the consumer from the diet over the lighter ^{14}N due to the preferential excretion of the lighter isotope (Peterson and Fry, 1987), which results in systematic enrichment of ^{15}N with trophic level (Kelly, 2000). This effect has been demonstrated in a number of different systems, with a variety of species. Mingawa & Wada (1984) observe step-wise enrichment of $3.4^{0}/_{00}$ ± 1 $^{0}/_{00}$, Fry of 3-4 $^{0}/_{00}$, (1988) and Hobson & Welch (1992) of 3.8 $^{0}/_{00}$ with each successive trophic level. It appears that the effect of trophic level enrichment can therefore be readily identified within a suitably defined range of values and that the highest value of $\delta^{15}N$ should correspond to the uppermost trophic level.

1.2.3.2 Carbon

The carbon isotope signature of biological material from marine sources appears enriched by ~ + 6.3 to + 7.9 $^{0}/_{00}$ compared to that of terrestrial/freshwater origin (Craig, 1953; Chisholm & Nelson, 1982; Mizuntani, 1990;). Such marked variation relates to the fundamental isotope ratio of the carbon source, as the two stable isotopes of carbon ^{13}C and ^{12}C fractionate at different rates depending on their biogeochemical environment (Hobson, 1986). Carbon is incorporated into the marine system as bicarbonate, CO_3, and into the terrestrial or freshwater environment as carbon dioxide, CO_2. The ratio of ^{13}C /^{12}C differs between these carbon reservoirs (Hobson, 1986; Bearhop *et al.*, 1999). Such isotopic source separation persists irrespective of trophic level. In addition, there is an observed +0.8 $^{0}/_{00}$ fractionation in $\delta^{13}C$ between an animal's whole body and its' diet (DeNiro & Epstein, 1978). Carbon enrichment of 1 $^{0}/_{00}$ per trophic level has also been observed in some marine systems (Hobson and Welch, 1992).

For any given trophic level dietary protein derived from terrestrial sources should vary in isotopic signature from protein of a marine source. Tissues from various sources have been used to successfully demonstrate the variation in isotope ratios relative to known freshwater/terrestrial and marine dietary sources (Chisholm & Nelson, 1982; Hobson, 1986, 1990).

Carbon isotopes have also been used to indicate the extent of bird feeding from freshwater and marine sources. Comparative analysis between $\delta^{13}C$ of known (baseline) whole food items (i.e. fish species) of known origin, and bird tissues (i.e.

bone collagen, feathers), have been used to demonstrate variation in isotopic signature between feeding locations. Using information that the average $\delta^{13}C$ for oceanic fish was (-17.5 $^{0}/_{00}$), 6.3 $^{0}/_{00}$ enriched compared to freshwater fish species (-23.8 $^{0}/_{00}$), Mizutani *et al.* (1990) measured the extent of feeding from the two aquatic systems using isotopic analysis of cormorant feathers (*Phalacrocorax carbo*). Hobson (1990), in measuring the extent of freshwater feeding in marbled murrelets (*Brachyramphus marmoratus*) demonstrated that predictions relating to feeding location could be extrapolated from stable isotope analysis of muscle tissue.

In more recent studies Bearhop *et al.* (1999) has supported this method of diet source determination by using a two-source mixing model based on cormorant feather isotope analysis referring to defined marine and freshwater 'end-points' to predict the extent of feeding in different locations.

1.2.3.3 Diet-tissue resource allocation

The process of how stable isotopes fractionate once they become incorporated into tissues has not been elegantly defined. Of course, this information is critical if tissues are to be used to accurately predict diet in species, as the extent of naturally occurring change in isotope representation will influence any estimates. However, it is recognised that the process of metabolism may produce a 1 $^{0}/_{00}$ enrichment in isotope representation, and this should be considered in any analysis (Hobson, 1990).

The rate of turnover of consumer tissue will also influence the isotope signature, and any estimate of isotope expression needs to identify potential rates of isotope assimilation into the tissue of interest. Tieszen *et al.* (1983) demonstrated in gerbils (*Meriones unguienlatus*) that ^{13}C turnover rates appear to be related to the metabolic activity of the tissue. Half-lives of carbon ranged: liver (6.4 days) < fat < muscle < hair (47.5 days). Therefore, it may be identified that the stable isotope composition of gerbil tissue provides a range of dietary information/time, depending on the tissue. Hobson (1992a, 1992b) used isotopes to explore the rates of tissue turnover in birds, using Japanese quail (*Coturnix japonica*) pectoral muscle, liver and humerus collagen. He revealed that half-lives of tissue showed a pattern similar Tieszens data: liver (2.6 days) < blood < muscle < collagen (173 days).

To measure the extent of isotope incorporation into tissue/time it is of paramount interest to use non-destructive sampling methods, i.e. by sampling blood or products of metabolism, so that temporal comparisons can be made on the same individual. Repeated blood sampling from captive American crows (*Corvus brachyrhynchos*) has been used to assess ^{13}C turnover (Hobson & Clark, 1993). However, sampling blood may not be practicable in the study of wild populations.

In birds, the production of an external fertilised egg offers a unique opportunity as it allows non-destructive, repeated sampling of a wild individual. It may be possible to use isotopes of recognisable signature to identify the extent of resource allocation from the females own body reserves to those in the developing egg. If the egg is biased in composition towards the females own tissue reserves, then egg isotope signature should reflect the long-term diet of the female bird. This acknowledges that the isotopes of the food source have been assimilated and transferred (via tissue metabolism and/or amino-acid turnover) into egg constituents.

In addition, eggs of a clutch are produced sequentially, and therefore temporal variation in isotope turnover may be revealed. Hence, it may be possible to follow a progressive change in resource allocation with time by 'tracking' the isotope of interest throughout the clutch sequence. By providing females birds with food of an isotope signature distinctly different to their wild diet isotope signature prior to laying, (during the period of egg formation), and analysing the resulting egg isotope composition, it may be feasible to predict the extent of diet/tissue contribution to the egg.

2 Aims and projected data analysis

Can the isotopic signature of egg tissue be used to make inferences about parental diet?

The overall objective will be to test the hypothesis that stable isotopes may be used to show evidence of nutrient transfer from diet to eggs, in birds feeding on diets of isotopically different origins (marine and terrestrial). Extending this, it aims to identify the following questions:

1) a) Is there a difference observed in the $\delta^{15}N$ and $\delta^{13}C$ stable isotope signatures of skua eggs between wild birds feeding on a catfood supplemented (treatment) diet of terrestrial origin, and those feeding on a natural marine (control) diet?
   b) If so, to what extent do eggs from the treatment group vary in isotopic composition?

A two-sample t-test (not assuming equal variance of the data) will be performed on the data to see if there are significant differences between the mean isotope values of all the egg data of catfood fed and unfed bird groups.

A one-way ANOVA will be employed to identify whether significant variation exists between treatment birds $\delta^{15}N$ and $\delta^{13}C$ signatures.

2) Is there evidence of a change in isotope expression in eggs as laying sequence progresses?

To identify whether there is evidence of sequential change in the extent of diet-egg isotope transfer, linear regression analysis will be applied to clutches of treatment and control birds, to see if there are significant patterns in isotope representation with laying sequence.

3) Can the amount of supplementary food incorporated into eggs be calculated using a two-source mixing model?

A mixing model will be generated graphically using isotopic signatures of known dietary source end-points and mean data from the treatment and control birds.

Lesser sandeels *Ammodytes marinus* will be assumed to represent the control diet of unfed birds (Furness, 1987), and catfood, the treatment diet of fed birds.

Catfood represents a single-step enrichment from the lowest trophic level of producer (grass based vegetation) to the cat food meat of the primary consumer (cattle and other herbivores). Catfood also contains plant material such as cereals and soya proteins (representing the signature of the primary producer). ^{15}N of the natural marine (fish) diet of the birds should represent a two-step trophic enrichment from the catfood, as the assumed sandeel-rich diet consists of sandeels feeding as secondary consumers of phytoplankton-fed zooplankton.

Suitable end points covering the proposed range of $\delta^{14}N$ and $\delta^{13}C$ end points are detailed in Table 1. Birds consuming a mixture of marine and terrestrial foods should have $\delta^{13}C$ tissue values linearly scaled between the known end-points. From the model it should be possible to measure the extent of feeding from each source in both bird groups. $\delta^{14}N$ values may be used as trophic level indicators.

Table 1. A range of isotopic values of $\delta^{13}C$ and $\delta^{14}N$ for various potential food items consumed by treatment (fed) and control (unfed) groups.

Source	Food Item	∂ 15 N (0/00)	Range	∂ 13 C (0/00)	Range	Source
'Marine'	Sandeel	7.9	5.9 to 9.3	-17.5	-16.5 to -18.5	Bearhop *et al.*, 1999
'Terrestrial'	Catfood	3.3	3 to 4	-25.5	-24.1 to -26.2	S Waldron (pers.comm)

Can the contribution of the supplementary food to the bioenergetic expenditure of the skuas be calculated?

The minimal energy expended to maintain body homeostasis during resting periods is known as the basal metabolic rate (BMR). The BMR of a large number of avian species has been studied (Klasing, 1998), and the value for great skuas has been calculated as 538 kJ/bird/day (Bryant & Furness, 1995). Although the BMR provides an estimate of energetic requirements at rest, a more useful measure is that of the field metabolic rate (FMR) which is the basal rate combined with the energy expended in such daily activities as feeding and locomotion. In breeding great skuas, FMR = BMR x 3.5 (Phillips *et al.*, 1999).

Using information about the FMR calorific requirements of skuas and the known calorific content of the catfood supplement, an estimate of the extent of catfood incorporated into the diet, and the bioenergetic value (kJ) of this contribution will be made.

In all analyses, the mean will be quoted, with its standard deviation value.

3 Materials and methods

3.1 Fieldwork and data collection

3.1.1 Fieldwork location

This study made use of eggs collected in 1999 during an experimental study of great skua *Catharacta skua* ecology. Fieldwork was undertaken by E Kalmbach and field staff on the island of Foula, Shetland (60°08'N, 2°05'W), during May and June 1999. The island supports a colony of around 2500 breeding pairs of great skuas (R Furness, pers. communication).

For the purposes of this study, the experimental group was formed of 12 pairs of birds, 6 of which comprised the treatment group. Individuals were recognisable by rings of unique colour combinations, also by individual variation in plumage.

3.2 Experimental protocol

The following outlines the methodology of the field work. Full details of field work methods can be found in Kalmbach *et al.*, (2001).

3.2.1 Supplementary food treatment

The treatment group consisted of 6 randomly selected breeding pairs of birds fed 400g of 'Safeway Savers' catfood daily, starting at least 10 days before laying commenced (starting May 1) and continuing until the last female ceased laying. It is assumed that females received the supplementary food irrespective of whether they or their mates had originally ingested it as male skuas provide for their mates by regurgitation (Furness, 1987). Food was distributed to the birds in the evening when almost all birds were on their territories. Great skuas energetically defend large territories which are well spaced (Furness, 1987) which should have prevented stealing of food by non-target birds. It should be noted that the food supplement did not replace the natural diet completely and that fed birds continued to forage. It has been shown in previous work on Foula that the provision of additional food prior to, and during egg production has no effect on egg size, clutch size, or lay date in great skuas (Kalmbach *et al.*, 2001).

Newly-laid eggs were removed from nests within 48 hours of being produced. Birds continued to lay and eggs were removed until the females ceased egg production. Egg removal induced birds to lay larger clutches than the normal clutch size of two eggs (Furness, 1987). Breeding pairs remained faithful throughout the experimental period (Kalmbach *et al.*, 2001).

3.2.2 Egg sample preparation

After 5 days of incubation the minute embryos were removed (for other analysis not considered in this study). The remainder of the eggs were frozen at - 20 °C until they were removed to Glasgow for analysis. Egg contents were thawed slowly and soft and hard parts separated before drying at 60°C until constant weight was achieved. The resultant dried contents were then mechanically ground using an electric grinder.

3.2.3 Laboratory procedure

3.2.3.1 Lipid removal

The isotopes in lipids are isotopically lighter in ^{13}C than whole body or protein values (De Niro & Epstein, 1978; Tieszen *et al.*, 1983; Hobson & Clark, 1992), and variation in their representation in tissues may complicate isotopic analyses. Therefore, it is usual for lipids to be removed from samples undergoing isotopic analysis.

It is possible to separate lipid from tissue samples due to the biochemical nature of the lipid components. The polar properties of lipid enable extraction of lipids from tissue by refluxing a suitable organic solvent over the sample until the solvent-soluble lipids have become biochemically incorporated into the solvent and hence removed from the sample. The solvent used must adhere to the following conditions: 1) being sufficiently polar to remove all lipids from their cell membrane or lipoprotein associations, 2) not so polar as to react chemically with the lipids, 3) not so polar that non-polar lipids remain, 4) must prevent enzymatic reactions (Christie, 1982). Chloroform is considered a suitable solvent to use thus was used in this analysis.

From a sub-sample of each egg the lipid content was removed using a Soxlet Apparatus. This resulted in a lipid-free and a lipid-rich sample originating from the same egg. It is

assumed that the reflux process removed all lipids and that the resulting lipid free samples consisted essentially of protein.

3.2.3.2 Isotope analysis using mass spectrometer

Mass spectrometry is the most widely applied method of isotope analysis (Elvidge & Jones, 1980). It is used to measure the abundance of isotopes in a sample by detecting and quantifying electronically the presence of ions in a minute sample of material that has been made gaseous. In brief, the substance under analysis is converted into gaseous form, subsequently ionised in a vacuum chamber and then accelerated through an electromagnetic field where the high-energy beam is resolved into components of differing mass/charge. The size of these differing beams can then be electronically counted and translated into relative abundance measurements (Criss, 1999). The ion source gas mass spectrometer in particular is useful for measuring small abundance and variation in such light stable isotopes as those of nitrogen and carbon (Criss, 1999).

3.2.3.3 Preparing and processing samples for isotope analysis

The coarsely ground egg samples were powdered further using a liquid nitrogen freezer mill (Spex Centiprep, Model 6750). Aliquots of each sample were placed into robust plastic vials containing a magnetic grinding rod. The vials were submerged in a bath of liquid nitrogen in the freezer mill, which rendered the sample more brittle and thus easily powdered when an alternating magnetic field was applied to the vial, moving the rod back and forward and grinding the egg to fine powder of isotopic homogeneity. (Note: catfood reference samples were hand-ground, using a pestle and mortar.)

For measurement of the carbon and nitrogen isotope ratio, approximately 0.44mg ($\pm$ 0.7mg) of this powdered egg was weighed using an Ultramicro balance (Sartorius) and loaded into tin cups (4 x 6mm). Isotopic analyses were carried out using a Finnigan Tracer Mat (Model NA1500) continuous flow isotope ratio mass spectrometer (CF-IRMS) coupled to a Carlo Erba C/N/S analyzer (Thermoquest, Hemel Hempstead, UK). This system combines sample conversion to carbon dioxide and nitrogen gases on-line to an isotope ratio mass spectrometer. Reference samples of known isotopic composition were run every five samples to correct for instrumental drift, and internal standards of know isotopic composition were run every ten samples to check for accuracy of drift correction. Known standards were incorporated into the combustion run to allow for correction of instrumental

drift if necessary. Both isotopes are considered in this study to give greater species segregation of the isotope signature than if only one isotope ratio is used.

The isotopic composition of a sample is reported in delta (δ) notation as parts per thousand ($^0/_{00}$) relative to an international standard and is calculated as follows:

$$\delta X = [\ (R_{Sample} / R_{Standard}) - 1\ ] \times 1000$$

where, X = the isotope under investigation (15 N or 13 C), and R = the corresponding isotope ratio of heavy : light isotopes 15N/14N or 13C/12C. $R_{Standard}$ for nitrogen is atmospheric air and for carbon is the Pee Dee belemnite (PBD) (which is a cretaceous belemnite (*Belemnitella americana*) from the PeeDee Formation of South Carolina. Repeat analysis of the internal standard shows accuracy and precision to be $\leq 0.2\ ^0/_{00}$ (S Waldron, pers. correspondence).

4 Results

4.1 Statistical analysis

4.1.1 Isotopic differences between treatment and control eggs

There was a significant difference between the clutches of treatment and control birds in both $\delta^{15}N$ and $\delta^{13}C$ signature. The eggs of fed birds showed nitrogen isotope depletion of 1 $^{0}/_{00}$ compared with the unfed group. The mean $\delta^{15}N$ isotope value for eggs was 9.9 (fed), 10.9 (unfed) ($t = -3.99$, $p = 0.007$, $DF = 6$) (Figure 1). Isotope depletion in ^{13}C was also observed, at - 0.9 $^{0}/_{00}$. The mean $\delta^{13}C$ value was –18.3 (fed), and –17.4 (unfed) ($t = -6.29$, $p = 0.000$, $DF = 8$) (Figure 2).

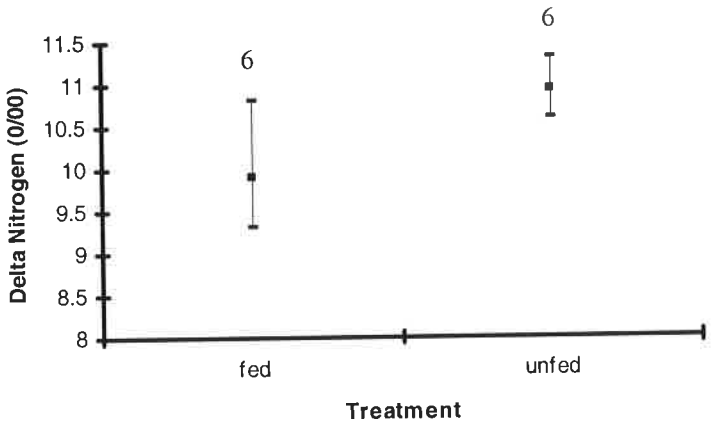

Figure 1. Variation in stable isotope values of $\delta^{15}N$ in catfood supplemented (fed) and wild feeding (unfed) great skua birds. Sample sizes are written above the data points. Means are indicated by solid squares and standard error by lines.

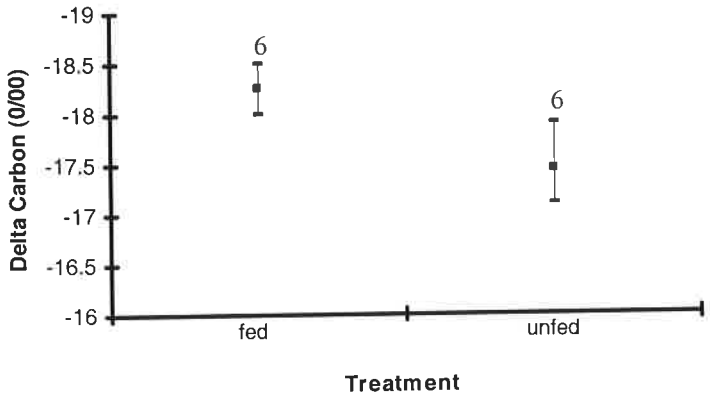

Figure 2. Variation in stable isotope values of $\delta^{13}C$ in catfood supplemented (fed) and wild feeding (unfed) great skua birds. Sample sizes are written above the data points. Means are indicated by solid squares and standard error by lines.

4.1.2 Isotopic variation between birds

A one-way ANOVA applied to all clutches of individual birds in the fed group revealed variation in mean $\delta^{15}N$ and $\delta^{13}C$ signatures (nitrogen: F = 3.15, p = 0.024, DF = 5; carbon: F = 6.14, p = 0.001, DF = 5) (Figures 3 & 4). The overall difference in the range of isotope signatures was $\delta^{15}N$: 2.4 $^{0}/_{00}$ (9.0 to 11.4 $^{0}/_{00}$) and $\delta^{13}C$: 1.2 $^{0}/_{00}$ (-17.7 to -18.9 $^{0}/_{00}$). Mean values ranged from 9.3-10.8 $^{0}/_{00}$ for $\delta^{15}N$, and –18.0 to -18.5 $^{0}/_{00}$ for $\delta^{13}C$.

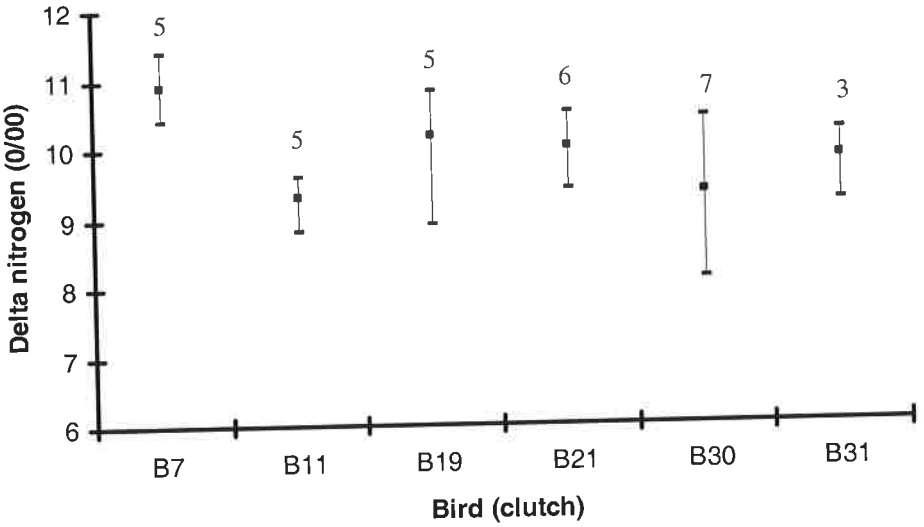

Figure 3. Variation in $\delta^{15}N$ between catfood supplemented (fed) great skua birds. Sample sizes are written above the data points. Means are indicated by solid squares and standard error by lines.

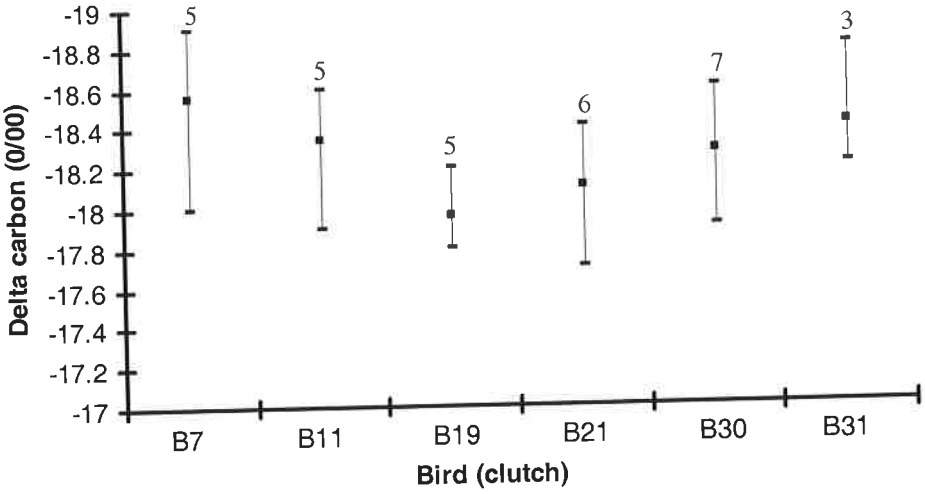

Figure 4. Variation in $\delta^{13}C$ between catfood supplemented (fed) great skua birds. Sample sizes are written above the data points. Means are indicated by solid circles and standard deviation by solid lines.

4.1.3 Isotopic variation within the clutches of fed birds

Regression analysis revealed that five out of the six birds of the treatment group showed no significant relationship between egg sequence and isotope signature. ^{15}N signature revealed a negative trend with egg sequence in four of the five birds, (birds 19, 21, 30 and 31) and a positive trend in bird 11. For ^{13}C, three birds displayed a negative trend in egg clutch and isotope signature (birds 11, 21 and 31) and two showed a positive association (birds 19 and 30).

One bird from the treatment group (bird 7) showed a significant negative correlation between laying sequence and egg signature in $\delta^{15}N$ ($r = 0.270$, $p = 0.004$, $n = 5$) (figure 5), and a positive trend in $\delta^{13}C$ (note: *y*-axis scale with increasingly positive $\delta^{13}C$) ($r = -0.210$, $p = 0.015$, $n = 5$) (figure 6).

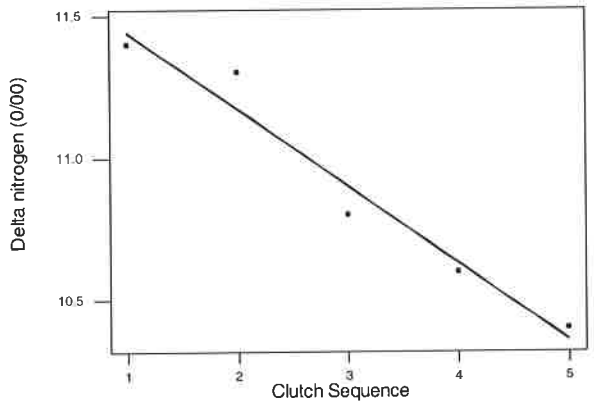

Figure 5. Regression of $\delta^{15}N$ and egg sequence in Bird 7

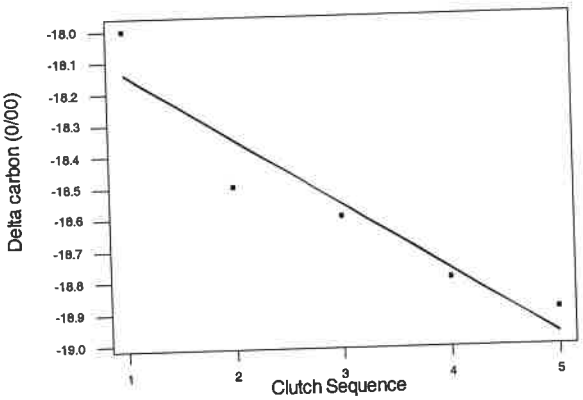

Figure 6. Regression of $\delta^{13}C$ and egg sequence in Bird 7

Of the control group, four out of five individuals from the treatment group showed no significant relationship between egg sequence and either isotope signature. ^{15}N signature revealed a negative trend with egg sequence in four of the five birds, (birds 51, 54, 57, 78 and 79) and a positive trend in bird 59. For ^{13}C, three birds displayed a negative trend in egg clutch and isotope signature (birds 51, 59 and 79) and two showed a positive association (birds 57 and 78). One control bird (Bird 54) showed a significant negative relationship between laying sequence and carbon isotope signature (note: *y*-axis scale with increasingly positive $\delta^{13}C$) ($r = 0.12$, $p = 0.029$, $n = 6$) (Figure 7).

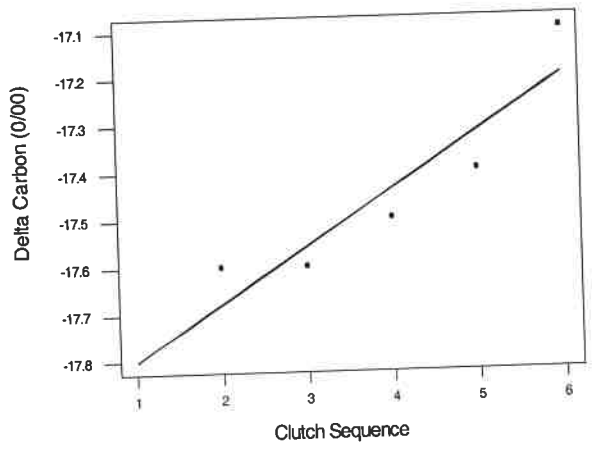

Figure 7. Regression of $\delta^{13}C$ and egg sequence in Bird 54

4.1.4 Two-source mixing model to calculate the extent of different dietary resources incorporated into the eggs

$\delta^{15}N$ and $\delta^{13}C$ signatures may be used to illustrate diet (catfood and sandeel, Table 1) and consumer (fed and unfed birds, Table 2) isotope signatures in the form of a two-source mixing model.

		Isotope signature (0/00)	
		∂ 15 N	**∂ 13 C**
Diet	Sandeel	7.9	-17.5
	Catfood	3.3	-25.5
Tissue	Unfed Eggs	10.9	-17.4
	Fed Eggs	9.9	-18.3

Table 2. A range of isotopic values of $\delta^{13}C$ and $\delta^{14}N$ for various potential food items consumed and the isotopic signature of eggs of fed and unfed birds.

The $\delta^{14}N$ and $\delta^{13}C$ values for skua eggs lie between the 'end-point' extremes of '100%' catfood and '100%' sandeel, depending upon the extent of incorporation of these food items. Unfed birds represent the signature of skuas assumed to be feeding almost exclusively on sandeels. Fed birds illustrate a signature related to both catfood and sandeel, as the total dietary protein contribution was derived from the two sources.

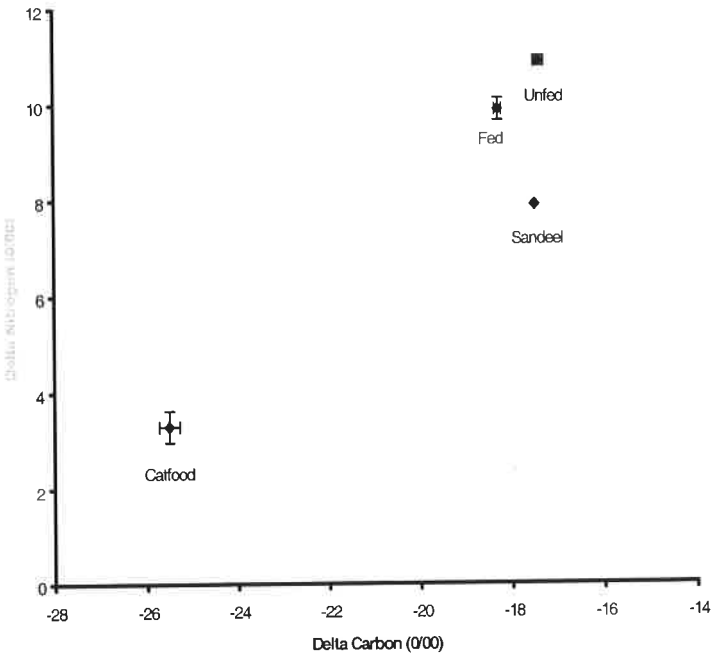

Figure 8. Mixing model to illustrate the extent of feeding of parent skuas from two different feeding sources. Means are represented by blue circles and standard error bars as solid lines.

From figure 8 it is immediately apparent that mean egg composition of fed birds relates more closely to the sandeel signature than that of the catfood. There is a greater difference between diet and (egg) tissue signature between catfood diet and the fed birds signature (^{14}N: +6.6 $^{0}/_{00}$ enriched, ^{13}C: +7.2 $^{0}/_{00}$ enriched), than sandeel diet and the unfed birds signature (^{14}N: +3 $^{0}/_{00}$ enriched, ^{13}C: +0.8 $^{0}/_{00}$ enriched). A small proportion of the difference in the signatures may be attributed to isotope fractionation between diet and the subsequent tissue. However, much of the difference observed between the catfood and egg signature of fed birds is, of course, related to the contribution the catfood makes to the total dietary input.

Calculating the contribution of each food item in fed birds using the dual-isotope multiple-source mixing model

It is possible to calculate the relative contribution of catfood in the diet of the fed birds. The model used is based on that developed recently by Ben-David *et al.* (1997) and used by Thompson *et al.* (1999). It uses the mean isotope signature of each consumed item (i.e. catfood), corrected by a fractionation factor to allow for naturally occurring isotope enrichment between the diet and the consumer (corrected values become A′, B′, etc…X′.). The correction values for the food item are calculated by applying a trophic level fractionation value of 3 $^{0}/_{00}$ for nitrogen, and a diet-tissue fractionation value of 0.8 $^{0}/_{00}$ for carbon (fractionation factors are according to the results of this study for sandeel diet and unfed birds, figure 8).

Using the Cartesian points of fed seabirds (F) and the corrected food items (A′, B′), the Euclidean distance of FA′ and FB′ can be calculated from the following equation:

$$z = \sqrt{x^2 + y^2}$$

The contribution that each food item (i.e. catfood) makes to the fed birds diet is inversely related to the distance between the corrected food item signature and the (fed) seabird signature. Therefore, the shorter the distance of FA′ or FB′, the greater the contribution of that item to the diet.

The calculation is as follows:

$$\% \text{ Contribution of food item, X} = \frac{FX'^{-1}}{(FA'^{-1} + FB'^{-1})} \times 100\ \%$$

where, X is A, B, etc. and X′ is A′, B′, etc.

Assumptions of the model are that the food items have significantly different isotope signatures, and that each individual (fed) seabird consumes all possible food items.

By these calculations, the contribution that the catfood supplement made to the diet is estimated at 11.9 %.

4.1.4 Contribution of catfood supplement to bioenergetic expenditure

The BMR (basal metabolic rate) value for great skuas has been calculated as 538 kJ/bird/day (Bryant & Furness, 1995). Additionally, in great skuas, the FMR (field metabolic rate) of an individual bird = 3.5 x BMR (Phillips *et al.*, 1999). To this end, the FMR (kJ) of a (breeding) pair of skuas can be obtained by the following calculation:

2 x 3.5 x 538 = 3766 kJ

By considering the calorific content of the catfood supplement, the bioenergetic value (kJ) of the catfood contribution to FMR can be made, and an estimate of the extent of catfood derived energy in the diet calculated.

The energetic value of 400g of catfood has been calculated as 1100kJ (Kalmbach, 2002, unpublished). Thus, the percentage contribution that catfood makes to the total energetic expenditure of a pair of skuas is calculated as (1100/3766) x 100 %, and estimated as 29.2 %.

5 Discussion

Isotope expression in eggs from birds of varying dietary protein isotope signature

The isotopic measurements of egg constituents from this study offer evidence that stable isotopes may be used to label dietary protein of different sources in the egg of the female bird, to measure the extent of incorporation of the protein in the laid clutch, and to define the relative proportions of food items in the diet from isotope signatures.

4.1.1 Differences in isotope signature between fed and unfed birds

There was significant variation between mean isotope signatures in both $\delta^{15}N$ and $\delta^{13}C$ between fed and unfed groups. The eggs of birds fed on the catfood supplement reflect incorporation of a terrestrial, primary consumer in their stable isotope signature.

Nitrogen: trophic level effect

The observed nitrogen isotope signature may represent a trophic level difference between fed and unfed birds. Variation in $\delta^{15}N$ is generally related to dietary differences with 3-4 $^{0}/_{00}$ enrichment accompanying each trophic step (Mingawa & Wada, 1984; Fry, 1988, Hobson & Welch, 1992). The catfood signature (3.3 $^{0}/_{00}$) was 4.6 $^{0}/_{00}$ depleted in $\delta^{15}N$ when compared to sandeel signature (7.9 $^{0}/_{00}$). Catfood represents a food item at the level of a primary consumer (consuming vegetation), whilst sandeels of the natural diet are secondary consumers (of zooplankton). Therefore, this separation of nitrogen isotope signature represents at least a one-step trophic level difference between catfood and sandeels. 1 $^{0}/_{00}$ depletion of $\delta^{15}N$ observed in the fed birds offers evidence that the fed birds were feeding on protein of a lower trophic level than the unfed birds.

Carbon: terrestrial versus marine

In addition, the catfood supplement of terrestrial origin appears to have depleted the carbon isotope signature of fed birds' eggs. The difference in $\delta^{13}C$ signature between the terrestrial catfood (-25.5 $^{0}/_{00}$) and marine sandeel (-17.5 $^{0}/_{00}$) was 8 $^{0}/_{00}$ which suggests clear freshwater-marine separation, according to previous work which has identified carbon isotope differences of tissue from freshwater to marine as 7.9 $^{0}/_{00}$ (Chisholm &

Nelson,1982). The observed shift of -0.9 $^{0}/_{00}$ in $\delta^{13}C$ of fed birds versus wild-feeding (unfed) birds suggests a terrestrial isotope contribution that has skewed the egg signature toward that of the –25.5 $^{0}/_{00}$ signature of pure catfood.

The extent of incorporation of the catfood isotopes is not pronounced because the catfood diet was only a supplement to the existing diet, and did not replace it completely. Therefore, the $\delta^{15}N$ does not reflect the 3-4 $^{0}/_{00}$ range (Mingawa & Wada, 1984; Fry, 1988, Hobson & Welch, 1992) recorded in previous studies and the $\delta^{13}C$ enrichment observed is minor.

Allocation of isotopes into egg from the diet

There was no evidence to suggest that isotope expression in the egg was either increasing or decreasing with continued egg production. Sequential increasing representation of the catfood signature with clutch sequence in fed birds would offer clear evidence that the catfood was being increasingly incorporated via one or more processes of resource allocation.

There was no relationship between the amount of catfood isotope signature and the egg sequence. Some birds showed a negative trend, and some a positive association. One fed bird (Bird 7) showed a significant decrease in $\delta^{15}N$ and increase in $\delta^{13}C$ in her eggs, which implies that catfood was becoming increasingly incorporated into the eggs. One explanation may be a switch in the source of the protein incorporated into the egg, from endogenous (sandeel-derived) reserves to directly from the diet. Alternatively, the catfood protein may be incorporated directly into the eggs, coupled with an increase in catfood digestion/tolerance (although all birds may have been observed to ingest the catfood, they may not have reacted favourably to the new diet initially, and later regurgitated and rejected the new food out of the sight of an observer). One bird (Bird 54) from the unfed group showed a significant negative relationship between laying sequence and carbon isotope expression in the eggs. This may suggest deviation from the sandeel diet towards an alternative source of protein of lower carbon signature, with increasing direct resource incorporation, as described above. However, significant results in these two individuals do not allow conclusions to be drawn about the wild population.

Ultimately, the extent to which the egg signature relates to that of the diet is influenced by the collective effect of the following:

- timing of egg production, in relation to the experimental period,
- potential transfer rate and method of transfer of dietary protein to egg,
- extent and duration of incorporation of the isotope within the birds system (in storage and use),
- the rate of naturally occurring fractionation, relating to the metabolic activity of the storage tissue in which the diet derived isotopes may be stored (i.e. muscle), also the tissue under investigation (egg)

The contribution of these factors cannot be separated in this investigation.

However, this isotope study clearly identifies that there is a particular resource allocation process (or combination of processes) that result in the transfer of food constituents into the laid egg. The egg has a signature related to that of the catfood. So, it is clear that the catfood signature becomes incorporated in the egg over the course of the pre-laying period of ca.10 days, although the process by which this is occurring is not easily defined.

Three processes relating to the source of the nutrients required for egg production have been proposed: 1) increase in dietary intake, 2) use of body reserves, 3) direct re-allocation of dietary resources to egg production (Houston *et al.*, 1995a). As the amount of catfood received by the fed birds was fixed, variation in the observed egg signature is due to the combination of one or all of these possible events. To this end, each will be discussed in turn, and its relative contribution evaluated.

The direct measurement of a possible increase in intake of the wild diet was not taken. Therefore, one does not know the extent, (if any), by which the birds compensated for continued egg production and the subsequent energy expenditure costs, in simply consuming more of their wild diet. Increasing dietary intake would presumably enable the female bird to mobilise her endogenous body reserves without loss of condition, and might affect the extent of direct dietary contributions towards egg formation. However, the reproductive period is a time of extended energetic cost (it represents time for oviduct enlargement and egg formation, as well as laying), and to rely entirely on the availability of a guaranteed additional food source near to the laying site would present a substantial risk for the laying bird. Therefore, increasing food intake as a result of increasing laying is unlikely to be the main source of nutrients directed towards egg synthesis. Despite this, it cannot be assumed

that birds did not consume increasing amounts of sandeel during continued egg production. Increased ingestion of sandeels might have directly influenced the egg signature in fed birds, as the proportion of sandeel : catfood would have increased. Therefore, although the amount of catfood distributed to fed birds was fixed, and the target bird pairs were observed to consume all the supplementary food offered them (E Kalmbach, pers. comm.), lack of information about individual birds foraging patterns may have contributed towards some of the observed individual variation.

The question remains as to whether the birds were using their own body reserves from selected organs to synthesise the eggs, or whether they directly re-distributed their immediate diet towards egg production. Either may be possible, and there is evidence that birds do use protein reserves when required, with muscle being a possible storage tissue (Kendall *et al.*, 1973; Jones and Ward, 1976). However, if the birds were mobilising protein reserves, they would have to be utilising a catfood-derived protein store in order for the signature to be observed as it was in the eggs. If endogenous reserves were the exclusive source of the egg nutrients, the storage of the diet constituents, subsequent breakdown and re-assimilation of the protein store would have to be taking place rapidly enough to occur over the experimental period. Such rapid 'shuttling' of nutrients might evoke high metabolic cost. The alternative strategy would be to prepare for the breeding and laying period by accumulating energy reserves in advance of actual need. However, this is also likely to involve cost, because of the additional locomotory effort required due to increased mass. It has been observed that breeding birds do not have sufficient nutrient reserves alone to enable them to fast completely whilst incubating eggs (i.e. brant (*Branta bernicla*) Ankney, 1984).

Birds may have been directly re-allocating the nutrients ingested as catfood towards egg production to some extent (i.e. some form of 'direct' amino acid transport from the digestive tract to the egg). If the final stages of egg production are rapid a direct contribution from the catfood diet at this time may result in an egg signature that reflects very faithfully the catfood intake.

It must be emphasised that the normal clutch size for great skuas is two eggs/pair. In removing eggs as soon as they were laid, birds were induced to produce further eggs. This may have added considerable physiological stress upon the birds, which may have had an influence on absorption efficiency of food constituents, and affected the mechanisms controlling resource allocation to eggs. The routine energy and protein metabolism of the

female bird may be affected during the lay period anyway (Houston *et al.*, 1995b). Therefore, placing the birds under such artificial physiological stress will have further disrupted the usual egg production processes.

The contribution of catfood to the diet and energy budget

The catfood signature represents only a small proportion of the signature of fed birds. Analysis using the two source mixing model estimates that the catfood contributes little more than $1/10^{th}$ (11.9 %) towards the fed birds eggs signature. It must be realised that calculation of this estimate incorporates catfood and sandeel isotope signatures as baselines depicting the potential range of catfood contribution to the diet. 'Sandeels' may not be representative of the wild diet of unfed birds. Wild seabirds may consume a range of different prey species (Bearhop *et al.*, 1999). Great skuas are known to consume fishing discards and other seabird fledglings (Furness, 1987), which will be of mixed marine and trophic isotope composition.

It has been estimated that catfood potentially contributes almost $1/3^{rd}$ (29.2 %) of the energy expenditure of breeding skuas. Catfood is typically composed of a selection of protein, carbohydrates and fat. Therefore, it must be noted that the energetic value calculated encompasses the contributions of all these components, and not protein exclusively.

Other factors contributing to the observed signatures

Wide variation in $\delta^{15}N$ and $\delta^{13}C$ was observed between individual birds. Although all the birds were from the same wild colony, a large proportion of the variation observed may be attributed to intraspecific differences between colony members. Although all categorised as 'adults', the individuals measured will inevitably represent different ages and years of reproductive experience. This should be considered as it has been identified that the fractionation values of avian tissues vary with age (Hobson and Clark, 1992b).

Perhaps more importantly, birds will have varied in their breeding condition prior to food supplementation. These factors may contribute to a range of ability within the experimental group to assimilate food, may influence the success and extent of foraging efforts, and could affect their ability to produce eggs of suitably comparable composition.

Additionally, there may have been energetic considerations affecting both groups of birds differently. Fed birds may have reduced their foraging activity due to the additional food source, which will have influenced their metabolic demands compared to the unfed birds. It should be noted that nutritional stress can result in higher $\delta^{15}N$ values (Hobson, 1992b; Kelly, 2000).

Future work

Stomach content analysis in combination with dual stable isotope analysis may be useful to support the results of further studies specific to dietary intake. In addition, measurements of more than one tissue type may be desirable to be able to investigate the possible changing relative contributions of different tissues over the reproductive period.

The measurement of whole tissues yields information on the integration of isotope contributions of all the various components that comprise that tissue. Each of these components will have their own characteristics influencing the isotopic composition (Hobson, 1992b). In the analysis of egg with lipid removed, the extent of dietary isotope potentially contributing to egg lipid has been ignored. Further analysis of eggs may be necessary to identify whether the dietary isotope signature can be identified in the lipid fraction.

Eggs are not metabolically inert but are experiencing rapid developmental processes that may vary the isotope signature of the egg over time. Thus, egg tissue may undergo compositional changes during synthesis and subsequent laying. It has been identified that there are significant differences in the carbon isotope signature of egg components from migratory double-crested cormorants (*Phalacrocorax auritus*) in those birds laying eggs earlier than others (Hobson *et al.*, 1997). It would be valuable to trace a recognisable isotope signature in the egg through various developmental stages, in an attempt to identify changes in the egg composition (and embryo). Any future use of egg tissue would benefit from further research into the fractionation rates of egg tissue components.

A source of protein will be only be adequate for egg production if it contains the correct balance of all essential amino acids (Houston *et al.*, 1995c; Houston, 1997). Therefore, can the amino acids essential for skuas be traced in wild birds from the diet to the egg? Labelled amino acids of dietary importance have been used to show the sequential transfer of amino acids from muscle to eggs in a (zebra finch) clutch (Houston *et al.*,1995c). The amino acid

requirements of captive skuas would need to be identified, in order to identify a useful amino acid tracer.

Conclusions

This study has demonstrated how a stable isotope approach may be used to provide quantitative information about the source of nutrients incorporated into the eggs of a wild bird population. Eggs may be a suitable short-term indicator of seabird diet where the sources of food are isotopically distinct and where there is baseline information about potential dietary contributions. Eggs represent a convenient method of isotope analysis that does not compromise the health of the adult bird, which may be of value in evaluating the diet of bird species of conservation importance.

Refinements in the use of stable isotope analysis to elucidate further the allocation of food source to egg, will offer an improved insight of foraging ecology in wild seabirds, during the breeding period. Thus, stable isotopes may be used to give valuable information pertaining to dietary change in seabirds, and may serve to contribute to the study of avian foodwebs in general.

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Appendices

Fed

Sample	∂ 15 N	∂ 13 C
FB997.1	11.4	-18.0
FB997.2	11.3	-18.5
FB997.3	10.8	-18.6
FB997.4	10.6	-18.8
FB997.5	10.4	-18.9
FB9911.1	8.8	-18.6
FB9911.2	9.5	-18.6
FB9911.3	9.6	-18.3
FB9911.4	9.3	-17.9
FB9911.5	9.3	-18.3
FB9919.1	10.2	-17.8
FB9919.2	10.8	-17.9
FB9919.3	10.2	-18.0
FB9919.4	10.7	-17.9
FB9919.5	8.9	-18.2
FB9921.1	10.2	-18.1
FB9921.2	10.3	-18.3
FB9921.3	10.2	-18.3
FB9921.4	9.7	-17.7
FB9921.5	9.4	-17.9
FB9921.6	10.0	-18.4
FB9930.2	10.4	-18.0
FB9930.3	9.5	-18.4
FB9930.4	9.8	-18.2
FB9930.6	8.1	-17.9
FB9930.7	9.2	-18.3
FB9930.8	9.4	-18.5
FB9930.9	9.0	-18.6
FB9931.2	10.2	-18.2
FB9931.3	10.1	-18.8
FB9931.5	9.2	-18.2

Bird	MeanN	MeanC
7	10.8	-18.5
11	9.3	-18.3
19	10.2	-18
21	10	-18.1
30	9.3	-18.3
31	9.8	-18.4
mean	9.892	-18.267

Unfed

Sample	∂ 15 N	∂ 13 C
FB9951.2	11.3	-17.5
FB9951.3	10.9	-17.6
FB9951.4	10.9	-17.3
FB9954.2	11.1	-17.6
FB9954.3	11.0	-17.6
FB9954.4	10.5	-17.5
FB9954.5	11.5	-17.4
FB9954.6	10.4	-17.1
FB9957.1	12.1	-17.7
FB9957.2	11.1	-17.8
FB9957.3	10.9	-18.2
FB9957.4	11.0	-18.1
FB9957.5	11.7	-17.7
FB9959.2	10.4	-17.7
FB9959.3	10.3	-17.5
FB9959.4	11.1	-16.9
FB9959.5	12.2	-17.3
FB9978.1	10.9	-17.4
FB9978.2	10.4	-17.5
FB9978.3	11.1	-17.8
FB9978.4	11.0	-17.1
FB9978.5	10.5	-17.3
FB9978.6	10.8	-16.8
FB9978.7	9.9	-17.3
FB9978.8	10.6	-17.0
FB9979.1	10.6	-16.9
FB9979.2	10.5	-17.2
FB9979.3	10.8	-17.0
FB9979.4	10.8	-16.8
FB9979.6	10.5	-17.5

Bird	MeanN	MeanC
51	11.0	-17.5
54	10.9	-17.4
57	11.3	-17.9
59	11.0	-17.4
78	10.7	-17.3
79	10.6	-17.1
mean	10.920	-17.421

Catfood samples

Sample	∂ 15 N	∂ 13 C
1		-25.9
2		-25.7
3		-25.7
4		-26.2
5	3	-25.1
6		-25.3
7	3	-24.1
8	4	-25.7
Mean	3.3	-25.5

from: S. Waldron

T-TEST: FED & UNFED BIRDS

NITROGEN

Two-Sample T-Test and CI: C_fed, C_unfed

```
Two-sample T for C_fed vs C_unfed

          N      Mean     StDev   SE Mean
C_fed     6   -18.267     0.186     0.076
C_unfed   6   -17.433     0.266      0.11

Difference = mu C_fed - mu C_unfed
Estimate for difference:  -0.833
95% CI for difference: (-1.139, -0.528)
T-Test of difference = 0 (vs not =): T-Value = -6.29  P-Value = 0.000  DF = 8
```

CARBON

Two-Sample T-Test and CI: N_fed, N_unfed

```
Two-sample T for N_fed vs N_unfed

          N      Mean     StDev   SE Mean
N_fed     6     9.900     0.573      0.23
N_unfed   6    10.917     0.248      0.10

Difference = mu N_fed - mu N_unfed
Estimate for difference:  -1.017
95% CI for difference: (-1.640, -0.393)
T-Test of difference = 0 (vs not =): T-Value = -3.99  P-Value = 0.007  DF = 6
```

ONE-WAY ANOVA

FED BIRDS

NITROGEN

One-way ANOVA: BIRD_N versus EGG

```
Analysis of Variance for BIRD_N
Source      DF        SS         MS        F        P
EGG          5     9.374      1.875     6.14    0.001
Error       26     7.944      0.306
Total       31    17.319

                                                Individual 95% CIs For Mean
                                                Based on Pooled StDev
Level       N      Mean     StDev  -+---------+---------+---------+-----
 7          5    10.900     0.436                          (-----*------)
11          5     9.300     0.308   (-----*------)
19          5    10.160     0.757             (-----*-----)
21          7     9.986     0.380           (-----*-----)
30          7     9.343     0.711    (-----*-----)
31          3     9.833     0.551         (-------*-------)
                                    -+---------+---------+---------+-----
Pooled StDev =    0.553          8.80      9.60     10.40     11.20
```

CARBON

One-way ANOVA: BIRD_C versus EGG

```
Analysis of Variance for BIRD_C
Source      DF        SS         MS        F        P
EGG          5    1.1694     0.2339     3.15    0.024
Error       26    1.9303     0.0742
Total       31    3.0997

                                                Individual 95% CIs For Mean
                                                Based on Pooled StDev
Level       N      Mean     StDev  --------+---------+---------+--------
 7          5   -18.560     0.351   (-------*--------)
11          5   -18.340     0.288           (--------*-------)
19          5   -17.960     0.152                    (-------*--------)
21          7   -18.100     0.252                (------*------)
30          7   -18.271     0.256             (------*------)
31          3   -18.400     0.346       (----------*---------)
                                    --------+---------+---------+--------
Pooled StDev =    0.272          -18.60    -18.30    -18.00
```

REGRESSION ANALYSIS

FED BIRDS

CARBON

```
Regression Analysis: Bird 7 Delta versus Egg Sequence


The regression equation is
Bird 7 Delta = -17.93 - 0.21 Egg Sequence

S = 0.130384      R-Sq = 89.6 %      R-Sq(adj) = 86.2 %

Analysis of Variance

Source          DF        SS         MS        F        P
Regression       1     0.441      0.441  25.9412    0.015
Error            3     0.051      0.017
```

Total	4	0.492

Regression Analysis: Bird 11 Delt versus Egg Sequence

The regression equation is
Bird 11 Delt = -18.73 + 0.13 Egg Sequence

S = 0.233095 R-Sq = 50.9 % R-Sq(adj) = 34.5 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.169	0.169000	3.11043	0.176
Error	3	0.163	0.054333		
Total	4	0.332			

Regression Analysis: Bird 19 Delt versus Egg Sequence

The regression equation is
Bird 19 Delt = -17.72 - 0.08 Egg Sequence

S = 0.0966092 R-Sq = 69.6 % R-Sq(adj) = 59.4 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.064	0.0640000	6.85714	0.079
Error	3	0.028	0.0093333		
Total	4	0.092			

Regression Analysis: Bird 21 Delt versus Egg Sequence

The regression equation is
Bird 21 Delt = -18.1467 + 0.0085714 Egg Sequence
S = 0.302922 R-Sq = 0.3 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.001286	0.0012857	1.40E-02	0.911
Error	4	0.367048	0.0917619		
Total	5	0.368333			

Regression Analysis: Bird 30 Delt versus Egg Sequence

The regression equation is
Bird 30 Delt = -17.9623 - 0.0554795 Egg Sequence

S = 0.230604 R-Sq = 32.6 % R-Sq(adj) = 19.1 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.128395	0.128395	2.41444	0.181
Error	5	0.265890	0.053178		
Total	6	0.394286			

Regression Analysis: Bird 31 Delt versus Egg Sequence

The regression equation is

Bird 31 Delt = -18.5429 + 0.0428571 Egg Sequence

S = 0.481070 R-Sq = 3.6 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.008571	0.008571	3.70E-02	0.879
Error	1	0.231429	0.231429		
Total	2	0.240000			

REGRESSION ANALYSIS

FED BIRDS

NITROGEN

Regression Analysis: Bird 7_Delta versus Egg Sequence

The regression equation is
Bird 7_Delta = 11.71 - 0.27 Egg Sequence

S = 0.101653 R-Sq = 95.9 % R-Sq(adj) = 94.6 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.729	0.729000	70.5484	0.004
Error	3	0.031	0.010333		
Total	4	0.760			

Regression Analysis: Bird 11_Delt versus Egg Sequence

The regression equation is
Bird 11_Delt = 9.06 + 0.08 Egg Sequence

S = 0.324551 R-Sq = 16.8 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.064	0.064000	0.607595	0.493
Error	3	0.316	0.105333		
Total	4	0.380			

Regression Analysis: Bird_19_Delt versus Egg Sequence

The regression equation is
Bird_19_Delt = 10.97 - 0.27 Egg Sequence

S = 0.721803 R-Sq = 31.8 % R-Sq(adj) = 9.1 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.729	0.729	1.39923	0.322
Error	3	1.563	0.521		
Total	4	2.292			

Regression Analysis: Bird _21_Del versus Egg Sequence

The regression equation is
Bird _21_Del = 10.3867 - 0.12 Egg Sequence

S = 0.300555 R-Sq = 41.1 % R-Sq(adj) = 26.4 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.252000	0.252000	2.78967	0.170
Error	4	0.361333	0.090333		
Total	5	0.613333			

Regression Analysis: Bird_30_Delt versus Egg Sequence

The regression equation is
Bird_30_Delt = 10.2339 - 0.159932 Egg Sequence

S = 0.627721 R-Sq = 35.1 % R-Sq(adj) = 22.2 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	1.06697	1.06697	2.70781	0.161
Error	5	1.97017	0.39403		
Total	6	3.03714			

Regression Analysis: Bird_31_Delt versus Egg Sequence

The regression equation is
Bird_31_Delt = 11 - 0.35 Egg Sequence

S = 0.187083 R-Sq = 94.2 % R-Sq(adj) = 88.5 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.571667	0.571667	16.3333	0.154
Error	1	0.035000	0.035000		
Total	2	0.606667			

REGRESSION ANALYSIS

UNFED BIRDS

CARBON

Regression Analysis: C_bird 51 versus Egg Sequence

The regression equation is
C_bird 51 = -17.7667 + 0.1 Egg Sequence

S = 0.163299 R-Sq = 42.9 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.0200000	0.0200000	0.75	0.546
Error	1	0.0266667	0.0266667		
Total	2	0.0466667			

Regression Analysis: C_Bird 54 versus Egg Sequence

The regression equation is
C_Bird 54 = -17.92 + 0.12 Egg Sequence

S = 0.0966092 R-Sq = 83.7 % R-Sq(adj) = 78.3 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.144	0.144000	15.4286	0.029
Error	3	0.028	0.009333		
Total	4	0.172			

Regression Analysis: C_Bird 57 versus Egg Sequence

The regression equation is
C_Bird 57 = -17.81 - 0.03 Egg Sequence

S = 0.265204 R-Sq = 4.1 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.009	0.0090000	0.127962	0.744
Error	3	0.211	0.0703333		
Total	4	0.220			

Regression Analysis: C_Bird 59 versus Egg Sequence

The regression equation is
C_Bird 59 = -17.98 + 0.18 Egg Sequence

S = 0.306594 R-Sq = 46.3 % R-Sq(adj) = 19.4 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.162	0.162	1.72340	0.320
Error	2	0.188	0.094		
Total	3	0.350			

Regression Analysis: C_Bird 78 versus Egg Sequence

The regression equation is
C_Bird 78 = -17.6286 + 0.0785714 Egg Sequence

S = 0.263222 R-Sq = 38.4 % R-Sq(adj) = 28.1 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.259286	0.259286	3.74227	0.101
Error	6	0.415714	0.069286		
Total	7	0.675000			

Regression Analysis: C_Bird 79 versus Egg Sequence

The regression equation is
C_Bird 79 = -16.8162 - 0.0824324 Egg Sequence

S = 0.262953 R-Sq = 32.7 % R-Sq(adj) = 10.2 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.100568	0.100568	1.45446	0.314
Error	3	0.207432	0.069144		
Total	4	0.308000			

REGRESSION ANALYSIS

UNFED BIRDS

NITROGEN

Regression Analysis: N_Bird 51 versus Egg Sequence

The regression equation is
N_Bird 51 = 11.6333 - 0.2 Egg Sequence

S = 0.163299 R-Sq = 75.0 % R-Sq(adj) = 50.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.080000	0.0800000	3	0.333
Error	1	0.026667	0.0266667		
Total	2	0.106667			

Regression Analysis: N_Bird 54 versus Egg Sequence

The regression equation is
N_Bird 54 = 11.26 - 0.09 Egg Sequence

S = 0.496320 R-Sq = 9.9 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.081	0.081000	0.328823	0.607
Error	3	0.739	0.246333		
Total	4	0.820			

Regression Analysis: N_Bird 57 versus Egg Sequence

The regression equation is
N_Bird 57 = 11.63 - 0.09 Egg Sequence

S = 0.574746 R-Sq = 7.6 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.081	0.081000	0.245207	0.654
Error	3	0.991	0.330333		
Total	4	1.072			

Regression Analysis: N_Bird 59 versus Egg Sequence

The regression equation is
N_Bird 59 = 8.83 + 0.62 Egg Sequence

S = 0.434741 R-Sq = 83.6 % R-Sq(adj) = 75.3 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	1.922	1.922	10.1693	0.086
Error	2	0.378	0.189		
Total	3	2.300			

Regression Analysis: N_Bird 78 versus Egg Sequence

The regression equation is
N_Bird 78 = 10.9714 - 0.0714286 Egg Sequence

S = 0.375436 R-Sq = 20.2 % R-Sq(adj) = 6.9 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.21429	0.214286	1.52027	0.264
Error	6	0.84571	0.140952		
Total	7	1.06000			

Regression Analysis: N_Bird 79 versus Egg Sequence

The regression equation is
N_Bird 79 = 10.6486 - 0.0027027 Egg Sequence

S = 0.175016 R-Sq = 0.1 % R-Sq(adj) = 0.0 %

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.0001081	0.0001081	3.53E-03	0.956
Error	3	0.0918919	0.0306306		
Total	4	0.0920000			

Calculating the contribution of each food item in fed birds using the dual-isotope multiple-source mixing model

The catfood isotope corrections, (3 ‰ for nitrogen, and 0.8 ‰ for carbon):

	Carbon	Nitrogen
Original value	-25.5	3.3
Corrected value	-24.7	6.3

Using the Cartesian points of fed seabirds and the corrected food items, the euclidian distances can be calculated from the following equation:

$$z = \sqrt{x^2 + y^2}$$

Euclidian distance between the fed birds and unfed:

	Carbon	Nitrogen
Fed	-18.3	9.9
Unfed	-17.4	10.9
Difference	0.9	1.0

$$\begin{aligned} Z &= \sqrt{x^2 + y^2} \\ &= \sqrt{0.9^2 + 1.0^2} \\ &= \sqrt{0.36 + 1.0} \\ &= \underline{1.166} \end{aligned}$$

Euclidian distance between the unfed birds and (corrected) catfood:

	Carbon	Nitrogen
Unfed	-17.4	10.9
Catfood	-24.7	6.3
Difference	-7.3	4.6

$$\begin{aligned} Z &= \sqrt{x^2 + y^2} \\ &= \sqrt{7.3^2 + 4.6^2} \\ &= \sqrt{53.29 + 21.16} \\ &= \sqrt{74.45} \\ &= \underline{8.628} \end{aligned}$$

The contribution that each food item makes to the fed birds diet is inversely related to the distance between the corrected food item signature and the (fed) seabird signature. Therefore, the shorter the euclidian distance between food item and consumer, the greater the contribution of that item to the diet.

The calculation is as follows:

% contribution of catfood :

$$= \frac{\text{unfed-catfood distance}^{-1}}{(\text{unfed-catfood distance})^{-1} + (\text{fed-unfed distance})^{-1}} \times 100\ \%$$

$$= \frac{8.628^{-1}}{(8.628)^{-1} + (1.166)^{-1}} \times 100\ \%$$

$$= \frac{0.1159}{0.1159 + 0.858} \times 100\ \%$$

$$= \frac{0.1159}{0.9739}$$

$$= 0.119 \times 100\ \%$$

$$= 11.9\ \%$$

The calculation for the contribution of catfood to the diet is as follows:

$$\%\ \text{contribution of food item, X} = \frac{FX'^{-1}}{(FA'^{-1} + FB'^{-1})} \times 100\ \%$$

where, X is A, B, etc. and X′ is A′, B′, etc.

Assumptions of the model: that the food items have significantly different isotope signatures, and that each individual (fed) seabird consumes all possible food items.

Activity budget and feeding behaviour of the North American porcupine, *Erethizon dorsatum*, in the Parc du Bic, Quebec, Canada

0110527j

September 2002

Submitted in part candidature of MRes. degree,

University of Glasgow

'Whether we look,
or whether we listen,

We hear life mumour,
or see it glisten.'

James Russell Lowell (1819-1891)

Abstract

Information relating to the behaviour of mammalian arboreal folivores is currently limited. Specifically, how the North American porcupine *Erethizon dorsatum* partitions its time during the night has not been documented. This study explored methods to study behaviour in porcupines, specifically in relation to foraging. Observations were carried out on seven female porcupines of a population in the Parc du Bic National Park, Quebec, Canada. After reviewing the data collected an activity budget for the porcupines was calculated. Inactivity was identified as the predominant behaviour, occupying 57% of observed time. Feeding was the dominant active behaviour (23% of observed time), and leaves of white spruce *Picea glauca* and trembling aspen *Poplus tremuloides* were identified as important food. Moving, travelling and vocalising were also observed to a lesser extent. Animals were identified as primarily arboreal folivores, with dietary specialisation on a narrow range of coniferous and deciduous tree species. How porcupines partition their time is discussed in the context of body form, metabolic rate, social behaviour and physiological adaptations, and some general comparisons are made between porcupine activity patterns and the time budgets of other arboreal folivores. This study provides a platform for future behavioural work on porcupines so that further work may place them in ecological context with other folivorous, arboreal mammals.

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Contents

1 Introduction

Interactions between an animal and its environment must ensure that nutritional requirements are met (Robbins, 1993) so that the animal is able to survive and function in performing long and short term activities contributing to its fitness. The distribution and availability of food items in the external environment undoubtedly influences a species evolutionary history, current distribution, and pattern of daily behaviour in its immediate habitat.

1.1 Herbivory trade-offs, constraints and adaptations

Generalist mammalian herbivores must manage their time effectively to enable them to subsist on a diet of vegetation, recognised as an abundant food source of general low nutritional quality due mainly to its high indigestible fibre content. The trade-off of low foraging costs in exploiting a plentiful supply of 'low-quality' material is that herbivores may need to allocate a considerable amount of time simply ingesting and digesting their food (Stephens & Krebs, 1986; Robbins, 1993). Digestive time constraints in processing bulky fibrous plant material may place physical limits on intake. In addition a diverse array of anti-herbivore plant secondary metabolites may influence foraging choices and incur metabolic costs that interfere with maximising energy intake. As a result, herbivores have evolved adaptations to enable them to process their diet efficiently. Specifically, these feature: dental adaptations of molars and premolars for shearing and grinding purposes, enlarged and specialised gastro-intestinal tracts allowing increased retention times of digesta (extended fore- and (or) hind-gut), complex detoxification pathways and employment of a diverse selection of symbiotic gastro-intestinal microflora to breakdown otherwise indigestible plant material by fermentation for subsequent assimilation (Kay & Hylander, 1978; Roze, 1989).

1.2 Arboreal folivores

Perennial plants are particularly vulnerable to predation by browsing animals as they represent a relatively predictable nutrient and energy supply in time and space. Therefore, trees and other plants are constantly evolving carbon-based chemical defences to compliment indigestible structural components in a co-evolutionary 'arms struggle' existing between plants and the animals that exploit them. For arboreal mammals consuming mainly tree foliage these chemical challenges are confounded by allometric

constraints of body size in an arboreal setting. There is a paradox between body size enhancing digestive ability yet restricting foraging capabilities (Cork & Foley, 1997). Because the capacity to digest plant material is dependent upon gut volume which in turn is dependent upon body size (Parra, 1978; Cork & Foley, 1997; Nagy, 1987) mammals <15 kg may face severe problems in meeting their energy requirements from folivorous diets due to the constraints of their small digestive system (Eisenberg, 1978). Indeed a body mass of <700 g is proposed to be the lower mass at which a mammal can survive on an exclusively folivorous diet (Jackson & Johnson, 2002). However large body size may restrict an animal's ability to forage efficiently arboreally. The vertical movements needed for climbing incur additional energetic costs in locomotion (Louw, 1993) and there are weight considerations. For an animal to maintain mobility in the canopy of trees upper mass limits of 15-20 kg have been proposed (Parra, 1978).

There are few examples of strictly arboreal and exclusively folivorous mammal species. Most leaf-eating mammals supplement their diet with seasonally available alternative foods such as insects, fruit, nuts and (or) seeds. However, feeding on small widely dispersed food items may become less efficient with increasing body mass due to the increased foraging effort and handling time required for a large animal to process sufficient numerous food items for its mass-related energetic requirements (Jackson & Johnson, 2002). Additionally a plentiful, constant supply of leaves is not available at all latitudes. Extreme seasonal fluctuations in temperature may limit plant productivity in northern ecosystems (Archibold, 1995). Most folivorous arboreal species are restricted to tropical climates where milder, more constant temperatures means trees provide a less variable source of food. Only 4% of all current 1135 mammalian genera contain species that are to some extent both arboreal and folivorous (Cork & Foley, 1997). Of 351 rodent genera, 5% have both arboreal and herbivorous adaptations (Eisenberg, 1978). To my knowledge the North American porcupine *Erethizon dorsatum* is the sole example of a temperate, folivorous mammal occupying a semi-arboreal niche. How it is able to maintain this position deserves further attention.

1.3 Daily activity budgets

Daily activity budgets offer behavioural quantification of how an animal partitions its time. Time is a constraint on the behaviour of animals and an individual must distribute available time among several important categories of behaviour (Matsumoto Oda & Oda, 1998). Activity budgets are influenced by diet and the distribution of food resources and also by

reproductive demands, home-range maintenance and physiological constraints such as ambient temperature (Jackson & Johnson, 2002). Short-term measurements of activity may offer information on habitat use and inter- and intraspecific interactions. Long-term studies may lead to insights of seasonal shifts in habitat utilisation and enable predictions to be made on how a species may be contributing to community-level changes.

1.4 Introduction to the study species

The North American porcupine has a wide geographical distribution throughout North America, in habitats ranging from desert-shrub to tundra (Appendix I: Map 1)(Roze, 1989; Tenneson & Oring, 1985). These semi-arboreal medium sized (7 kg) rodents although considered generalist herbivores, are primarily folivorous, browsing on a range of ground vegetation and both deciduous and coniferous tree species (reviewed in Roze, 1989). The animals exhibit seasonal dietary selectivity with an exclusive winter diet of the inner (cambium) layer of tree bark and evergreen needles (Snyder & Linhart, 1997; Tenneson & Oring, 1985; Vispo & Hume, 1995), spring forage consisting of some ground vegetation and new buds (Curtis & Kozicky, 1944), a summer diet of tree leaves, and autumn feeding both in trees and on ground vegetation (Roze, 1989). Porcupines are largely solitary although the home range of animals may overlap. Females may show some gender-specific territoriality towards other females, and strong site-fidelity (Roze, 1989).

To date, information on North American porcupines is limited. Their behavioural ecology remains poorly understood, and many accounts of porcupine behaviour are anecdotal (Curtis & Kozicky, 1944; Roze, 1989). Early work focussed broadly on the potential economic impact of foraging behaviour, as the animals winter diet may encompass commercially important tree species (such as Eastern hemlock *Tsuga canadensis* and ponderosa pine *Pinus ponderosa*), and sublethal damage to the bark of trees in winter may affect subsequent radial growth causing disfigurement, and potentially increase infection to disease and insect infestation (Curtis & Kozicky, 1944; Spencer, 1964; Ilse & Hellgren, 2001). Further work has investigated nutrient requirements and digestive capabilities (Vispo & Hume, 1995; Fournier & Thomas, 1997; Felicetti *et al.*, 2000).

2 Aims and projected data analysis

The overall objective was to devise a suitable method to quantify the behavioural activity of porcupines within their forest habitat, and to evaluate how the resulting activity budget places North American porcupines in ecological context amongst other herbivores, specifically arboreal folivores.

2.1 Nocturnal activity patterns: preliminary analysis

Aim: to explore the quality of data available for further analysis

An overview: to what extent is porcupine behaviour observed during the night?

Initial analysis summarised data from focal observations over a 12 hour period of the night (18:00-5:00). At the level of the individual focal porcupine (n=7) the Chi-squared test was used to identify whether animals differed in the amount of time they were observed versus unobserved during the focal night. Chi-squared was further used to explore differences between individuals in the minutes of active and non-active behaviour during periods of observation.

During which hours of the night is activity recorded?

It was necessary to identify the period of the night during which data was collected for the majority of focal animals, *i.e.* good representation of behavioural data. Pooling all focal observations (n=12) the number of porcupines engaged in one or more minutes of active behaviour across the hours was displayed graphically. This interpretation of the data offered a general overview of the incidence of active behaviour between 18:00 and 5:00.

During which hours of the night are most observations on behaviour recorded?

The number of porcupines observed (active or inactive) for 30 minutes or more each hour of the night were calculated and the Chi-squared test applied to identify whether there were significant differences between hours of the night and the number of porcupines observed during each hour (n=12). This aimed to highlight the period of the night that would be most suitable for further data analysis.

2.2 An activity budget for *Erethizon dorsatum*

Aim: to define nocturnal patterns in porcupine behaviour

A brief review of the methodology used

The Chi-squared test was used to identify whether there were significant differences between porcupines in the methodology used to record data between the best represented hours (n=7).

How is observed behaviour distributed throughout the most data-extensive period of the focal night?

Over the most 'data-extensive' hours of the night the percentage of porcupines engaged in one or more minute of each behaviour (inactive, feeding, moving, travelling and vocalising) was calculated from the median of all individual animals (n=7). Subsequently, the Kruskal Wallis test was used to identify whether there were differences, *i*) in the incidence of behaviour across hours of the night and *ii*) within each hour.

What is the distribution of observed behaviour during this period of the focal night?

The extent of observed versus unobserved minutes of behaviour across all hours was tested using the Mann Whitney U test to compare medians (n=7). Subsequently, the Kruskall Wallis tested differences across the hours (n=7).

What is the extent and distribution of behaviour during this period of the night as a proportion of observed time?

The Kruskall Wallis was used to consider differences between the median percentage representation of behaviours across the whole night (n=7) and then used again to test differences between and within hours of the night (n=7).

2.3 Foraging behaviour

Aim: to explore tree use and foraging preferences

How were the trees used in which porcupines were found?

A graphical overview of tree use was followed by the Chi-squared test applied to the number of 'deciduous' and 'coniferous' type trees fed and not-fed upon by porcupines to identify whether porcupines were targeting specific tree types for feeding purposes (n=12). Chi-squared was further used to explore whether there was a significant association between hour and the number of descents recorded within that hour (n=21).

What is the porcupine's dietary breadth of tree species and can tree foraging preferences be inferred?

The number of different tree species porcupines were observed foraging upon offered an overview of dietary range. The contribution of different species consumed as a percentage of all species fed upon was displayed graphically.

How do other species of plant contribute to dietary breadth?

There was a brief overview of the incorporation of food items into the diet that may offer an alternative to tree leaf browsing.

Minitab (Version 13) statistical software was used in all computer aided statistical analysis.

This study expanded work undertaken by Masters student Patrick Morin in 2001 which identified that resident porcupines were most active between dusk and dawn (unpublished, Morin & Berteaux), supporting general knowledge that porcupines are predominantly nocturnal (Roze, 1989). It was on the basis of this information that data was collected over the night (and diurnal activity was not considered).

In recognition that sample sizes were small, (12 observation nights, seven individuals), non-parametric tests were applied to the data throughout. Although non-parametric tests reduce the chances of a Type I Error when sample sizes are small it is generally considered that parametric tests have more statistical power (but see Martin & Bateson, 1995). Hence although significant results described in the analyses of this data are likely to be genuine, small sample sizes mean that significant differences may not have been detected in the first place (Dytham, 2001).

Where there were repeated observations (focals) on the same individual, mean values were used to generate average values per porcupine. All subsequent summary statistics were quoted as medians unless described otherwise.

3 Materials and Methods

3.1 Fieldwork location

This research was carried out within the National Park of Parc du Bic, Quebec, Canada, (48°19′-48°22′ N, 68°42′-68°47′ W), located approximately 290 km north east of Quebec City (Appendix I: Maps 2 & 3). The 33.2 km^2 park is situated on the south shore of the St. Lawrence basin, with a maximum elevation of 346 m. The 2 km^2 study area consisted of a combination of forest, arable farmland, salt marsh and rocky shore habitat typical to the park. The region is dominated by mixed forest, with principal tree species of balsam fir *Abies balsamea*, balsam poplar *Poplus balsamifera*, trembling aspen *Poplus tremuloides*, white birch *Betula papyrifera*, white cedar *Thuya occidentalis* and white spruce *Picea glauca.* Air temperature ranged from 2° C to 31° C (approximately) over the course of the data collection period.

The porcupine population of the Parc du Bic study area has been monitored since 2000 (principally by students of the University of McGill and the University of Quebec at Rimouski). This study describes data collected on seven adult female porcupines between 8 May and 3 July 2002.

Table 1. Biometric data collected from porcupines captured on the study area of Parc du Bic National Park, Quebec. Measurements were taken from 2002 capture data as follows: Body mass – weight was recorded using a 100 g spring balance (Pesola AG, Baar, Switzerland); Body length – base of the nose to the tip of the tail; Mean chest width – width of the ventral surface of the animal, between the front legs; Hind foot length and breadth – surface of the foot pad at longest and broadest point. Note: All measurements were taken whilst the animals were under sedation and therefore in muscular relaxation. Data describes actual values or means from multiple captures with corresponding standard deviations in parentheses.

Focal individual	Date of first capture	Mean body mass (kg)	Mean body length (cm)	Mean chest width (cm)	Mean hindfoot length (cm)
A	July-00	6.0 (0.44)	71 (-)	49.5 (-)	6.3 (-)
B	May-00	7.8 (0.67)	72 (0.35)	54 (7.07)	6.6 (-)
C	May-00	6.5 (0.6)	72 (0.45)	56.7 (3.51)	6.4 (2.65)
D	May-00	5.6 (-)	-	-	-
E	May-01	8.7 (0.59)	74 (-)	50 (-)	6.3 (-)
F	May-00	5.7 (0.71)	69 (-)	51 (-)	6.0 (-)
G	June-00	6.9 (0.52)	74 (-)	49 (-)	6.3 (-)
Mean (SD)		6.7 (1.15)	72 (1.9)	51.7 (3.03)	6.3 (0.19)

3.2 Data collection

The focal individuals used in this study were captured at night by systematic searching using hand-held nets, fitted with 60 g radiotransmitting collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) under mild sedation (using a combination of Ketamine (0.1ml/kg) and Xylazine (0.2ml/kg)) and then released. Subsequent radiotracking was carried out using a hand-held yagi antenna (model F172-3 FB, AF Antorinics Inc., Urbana, Illinois, USA) with a telemetry receiver (model R-1000, Communication Specialists Inc., California, USA). Animals carrying collars showed no obvious signs of discomfort or abnormal behaviour.

For each focal, the target animal was located before dusk (18:00–21:00) and their behaviour followed over an average of 9 hours until after dawn (4:00– 6:00). During each focal period, the occurrence of all predetermined activity categories were recorded continuously when available (according to Martin & Bateson, 1995). Each animal was observed for a maximum of two nights. For independence of observations the same porcupine was not observed on successive nights. Data analysed includes 110 total focal hours for seven individuals over 12 focal nights.

A combination of visual, audible and radio-telemetry techniques was used to collect the data. Binoculars (10 x 50 magnification) or a monocular night-vision apparatus (model Wolf II, Moonlight Products, High Wycombe, Buckinghamshire, UK) was employed wherever possible for direct observation of the focal animal, auditory data was collected when visual observation was obscured and radio-telemetry was necessary when both visual and audible data was unavailable. For radio-telemetry observations, the telemetry receiver LED display showed a variable visual signal when the focal animal was moving (*i.e.* active), and a constant signal when the animal was stationary (*i.e.* inactive). Telemetry checks were carried out discontinuously at 5-minute intervals. Hence, although telemetry data did not provide detail of the specific activity of the focal individual, it provided an adequate means of discriminating between whether an animal was active or inactive when out of sight or earshot.

Active behaviour was classified in the following way and recorded in minutes:

- *Feeding:* The animal was engaged in the preparation and ingestion of any food item. (Recorded using visual and audible methods);
- *Vocalising*: The animal emitted audible vocal sounds not related to feeding. (Audible);
- *Travelling*: Movement other than shifts in position related to feeding and vocalisation. (Visual and audible);
- *Moving*: Locomotor activity related to feeding, vocalisation or shifts in position. (Visual, audible and radio-telemetry).

Note: *Inactivity* could be calculated from active time by subtracting active minutes from total observation time.

For the purposes of analyses, in the event of an animal switching its behaviour (*e.g.* feeding to vocalising) during the same minute, the resultant 'new' activity was recorded (*i.e.* vocalising, in this example). Similarly, when an animal performed more than two activities during the same focal minute (*e.g.* feeding, vocalising and travelling) the first activity to be recorded was used in subsequent analyses.

Each focal night commenced by a telemetry search to visually locate the focal porcupine. Behaviour was recorded continuously until the animal moved such that a reliable location estimate (*i.e.* ground or tree) was considered unobtainable. After a 20 minute delay to allow the porcupine to 'escape' a telemetry search ensued, until the animal was relocated. In this fashion, focal nights consisted of observation periods of active and inactive behaviour punctuated with non-observation periods (mainly telemetry searching) when no data was collected. The result was a temporal record on bouts and durations of behaviour at known locations interspersed with episodes when behaviour and location was unknown.

In an attempt to reduce observer impact on the animal's behaviour a red filter was used on the headlamp equipment (Petzl Zoom, Lyon Equipment, Cumbria, UK) to reduce light intensity (see Jackson & Johnson, 2002) and headlamp use was minimal. A wristwatch light provided illumination for recording data, and the headlamp was used only to aid navigation when locating the animals. Reducing light disturbance was considered important as resident porcupines may be developing sensitivity to artificial light, (personal communication, J Roberge & D Berteaux) as they are located with high intensity (1000 lux) spotlights prior to being captured (for purposes not considered in this study).

4 Results

4.1 Nocturnal activity patterns: preliminary analysis

4.1.1 An overview: the extent that porcupine behaviour was observed during the focal night

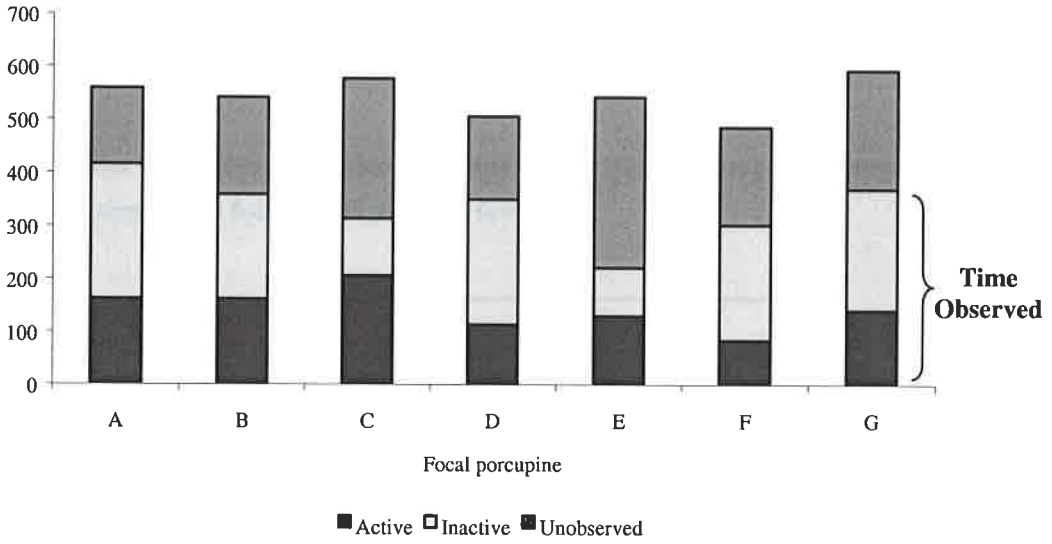

Figure 1. Mean observed (active and inactive) and unobserved focal time (minutes) for each focal porcupine (animals labelled A-G) (n=7)

Median focal night length was 542 minutes (range: 485 to 592 minutes). Porcupines were observed (active or inactive) for a median of 30% more time than they were unobserved. Median observation time was 349 minutes (64% of total focal time) and median unobserved time was 184 minutes (34%).

However there was significant variation in observed time relative to unobserved time between animals across the night (χ^2=313.7, df=6, P<0.001) (Figure 1). Although samples sizes were insufficient to statistically test the difference observed between animals inferences can be made on where differences may lie. In six out of the seven focal animals behaviour was observed for more time than it was not observed. Porcupines A, B, C, E, F and G were all observed for more than 50% of the focal night. One animal (A) was observed for 74% of the night (416 out of 559 mean focal minutes). In contrast, another animal (D) was observed for only 41% of focal time (221 out of 542 minutes).

During observed time porcupines were recorded inactive a median 14% more time than they were seen active. Inactivity was recorded for a median 217 minutes which represented 40% of the focal night (60% of observed time), whilst active bouts constituted a median 141 minutes or 26% of focal time (40% of observed time). Again, there were differences across the night between individuals, with a significant deviation from the minutes expected had observed time been divided equally between activity and inactivity (χ^2=225.8, df=6, P<0.001). Five out of the seven porcupines spent more time inactive than active during observed periods. However two animals (porcupines C and E) show the reverse, and were both active for more time than inactive.

Table 3. Number of minutes porcupines were observed in tree, ground and unknown locations during total observed time for all focals (1796 minutes) (*n*=12)

Observed time	Location		
(minutes)	Tree	Ground	Unknown
Total	1528	260	8
%	85.1	14.5	0.4

The majority of observation data describes porcupine behaviour whilst the animals were in tree locations (Table 3). 85% of all observation time (1528 minutes) observations were made when animals were located in trees compared to 14% (260 minutes) when animals were located on the ground (Table 3).

4.1.2 Hours of the night during which activity was recorded

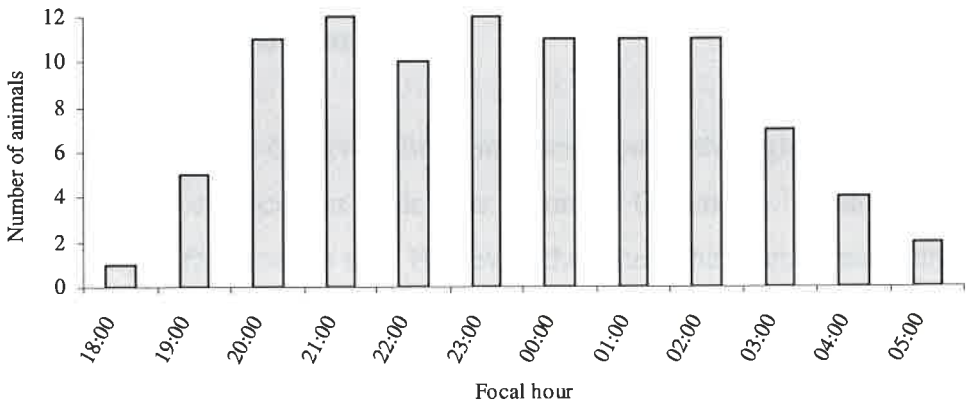

Figure 2. The number of porcupines engaged in one or more minutes of active behaviour during each focal hour throughout the night (18:00-05:00) (*n*=12)

One or more minute of active behaviour in porcupines was recorded during all hours throughout the focal night (Fig.2). The number of focal animals active each hour ranged from 1 (8% of all animals) to 12 (100%). Figure 2 illustrates that between the hours of 20:00 to 2:00 activity was recorded in at least 10 animals per hour.

4.1.3 Hours of the night during which most observations on behaviour were recorded

The previous representation of activity incidence per hour does not define the extent of porcupine activity within each hour. Duration of activities within an hour could range from one to 60 minutes. Therefore hours of the night were sub-divided into 30-minute periods describing whether animals were observed (either active or inactive) during each 30-minute bout, to identify the extent of porcupine observations during each hour.

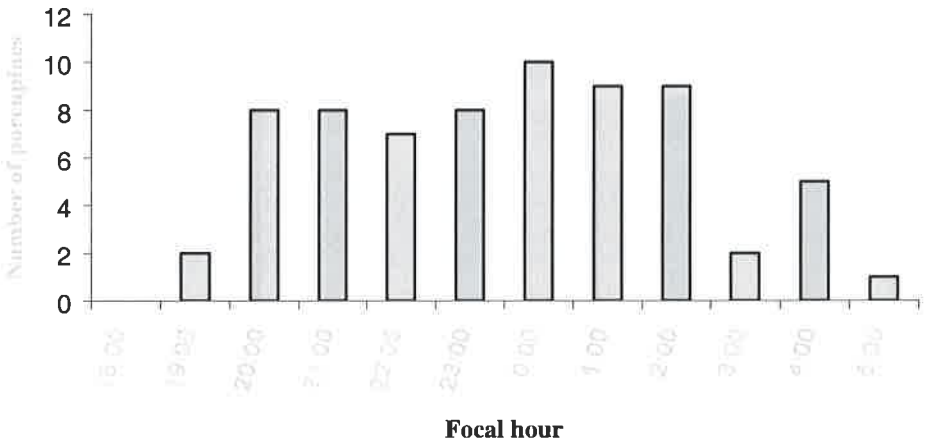

Figure 3. The number of porcupines observed for at least 30 minutes during each focal hour throughout the night (18:00-05:00) (n=12)

Fewer porcupines were observed for 30 minutes or more throughout hours of the night than where activity incidence per hour was recorded (Figure 3). The number of animals observed ranged from one to ten. However, the extent that porcupines were observed was not distributed equally over all hours. Over the whole night (18:00-5:00) there were significant differences between hours in the number of porcupines observed during each hour ($\chi^2 = 46.8$, df=11, P<0.001). Figure 3 shows no animals observed (for 30 minutes or more) at 18:00 and fewer than 50% of all porcupines observed each hour during 19:00, 3:00, 4:00 and 5:00. It appears the hours providing extensive observation data generated

from the greatest number of individuals (seven or more animals) are restricted to between 20:00 – 2:00. There was no significant difference between the number of porcupines observed and unobserved within and between these hours (χ^2=2.3, df=6, P=0.892). In recognition of this, the following analyses of behaviour describe data from this period of the night only.

4.2 An activity budget for *Erethizon dorsatum* (from behavioural observations between 20:00 and 2:00)

4.2.1 A review of the recording methods used to collect focal data

Between 20:00 and 2:00 not all observation data was collected by the same methods. Audible methods (listening to behaviour) were the most frequently used recording technique and was used to record a median 68% of behaviour. Visual observations accounted for a median of 28% of observation time and telemetry was used only 5% of the time.

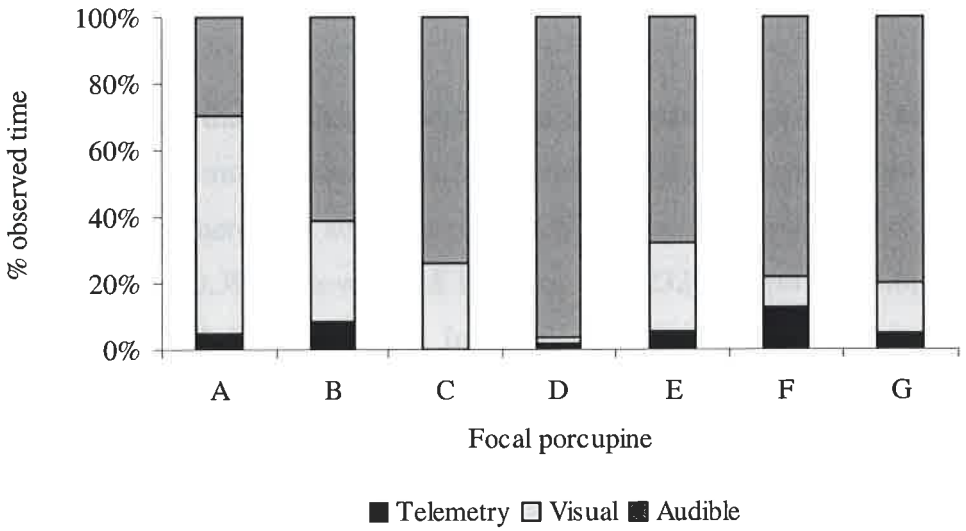

Figure 4. The percentage of observation time that different recording methods were used during each focal 20:00-2:00 (*n*=7)

However there was a significant difference between porcupines in the number of minutes that different recording methods were used as a proportion of each animals observed (recorded) time (χ^2 =300.8, df=12, P<0.001) (Figure 4). Large differences may lie between the techniques used for porcupines A and D. 66% of behaviour was recorded for animal A by visual observations and 30% by audible signs. By contrast, audible observations were used for 96% of observations on animal D, and only 2% were collected by visual methods.

4.2.2 The general distribution of behaviour

It was not practicable to divide the night into 30-minute periods of different behaviours (as applied previously, see Figure 3) because most bouts of individual behaviours were insufficiently long. Therefore, the following overview considers incidence of behaviour per hour as one or more minute of behaviour. All behaviours *(inactivity, moving, feeding, vocalising and travelling*) were represented for one minute or more during each hour of the 20:00-2:00 period (Figure 5).

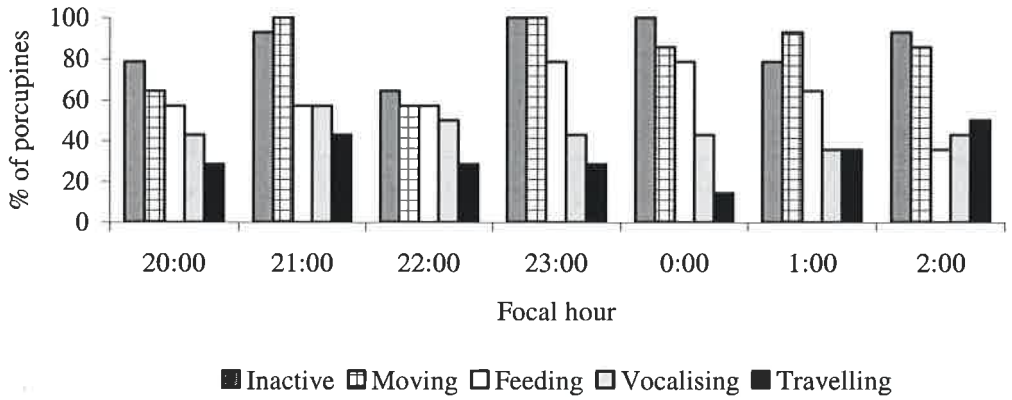

Figure 5. The percentage of porcupines engaged in different behaviour between hours 20:00-2:00 (*n*=7)

Across the night the number of porcupines (as a percentage of all seven individuals) engaged in one or more minute of each behaviour did not vary significantly between hours (Kruskal Wallis (hereafter abbreviated to KW), Inactive: H=5.3, df=6, P=0.505; Feed: H=6.3, df=6, P=0.396, Move: H=8.1, df=6, P=0.232; Travel: H=3.6, df=6, P=0.730; Vocal: H=1.8, df=6, P=0.937). Inactivity and moving were the most frequently documented behaviours, with a median 93% of animals observed not engaged in any active behaviour for one or more minutes per focal hour and 86% moving. Of other behaviours, a median 57% of porcupines were feeding each hour, 43% vocalising and 29% travelling. This demonstrates almost 66% more animals recorded inactive each hour compared to the least documented behaviour of travelling.

However within each hour of the night there were significant differences in the percentage of porcupines engaged in different behaviours during 21:00 (KW, H=13.8, df=4, P=0.008), 23:00 (KW, H=3.9, df=4, P=0.426), 0:00 (KW, H=19.8, df=4, P=0.001), 1:00 (KW, H=10.6, df=4, P=0.031) and 2:00 (KW, H=11.5, df=4, P=0.022). Clear differences between the representation of behaviours during these hours can be observed in Figure 5.

However, during 20:00 and 22:00 the difference in the percentage of porcupines engaged in different behaviour was not significant (KW, 20:00: H=6.7, df=4, P=0.150; 22:00: H=3.9, df=4, P=0.426). During these two hours feeding, vocalising and travelling behaviour seem represented similarly to other hours, although it appears fewer porcupines were seen inactive and moving.

4.2.3 An overview: observed versus unobserved behaviour

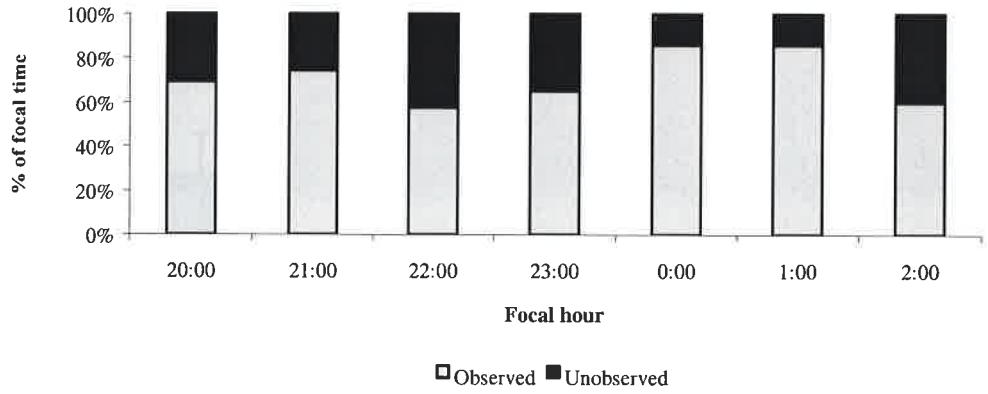

Figure 6. The percentage of time (minutes) that porcupines were observed and unobserved during all hours between 20:00-2:00 (*n*=7)

Between 20:00 to 2:00 porcupines were observed for more time than they were unobserved and the difference between median percentages of observed and non-observed time (minutes) was significant (Mann Whitney U. W=77.0, df=6, P=0.0021) (Figure 6). The median observation time (mean data from individuals combined) was 69% of focal time (290 minutes), and median unobserved time 31% (130 minutes). There was no significant difference in the median amount of time animals were observed across hours of the night (KW, H=3.5, df=6, P=0.740).

The extent of time each porcupine was unobserved during every hour was used to extrapolate the number of minutes an animal participated in behaviour as a proportion of the observed time. The following figures and analyses of behavioural data relate to suitably adjusted data.

4.2.4 The extent and distribution of behaviour as a proportion of observed time

Different behaviours were not represented equally during the 20:00 to 2:00 focal night (Figure 7). In relation to observed time the median percentage of time porcupines spent engaged in different behaviours across the whole night was significantly different for each behaviour (KW, H=26.1, df=4, P<0.001).

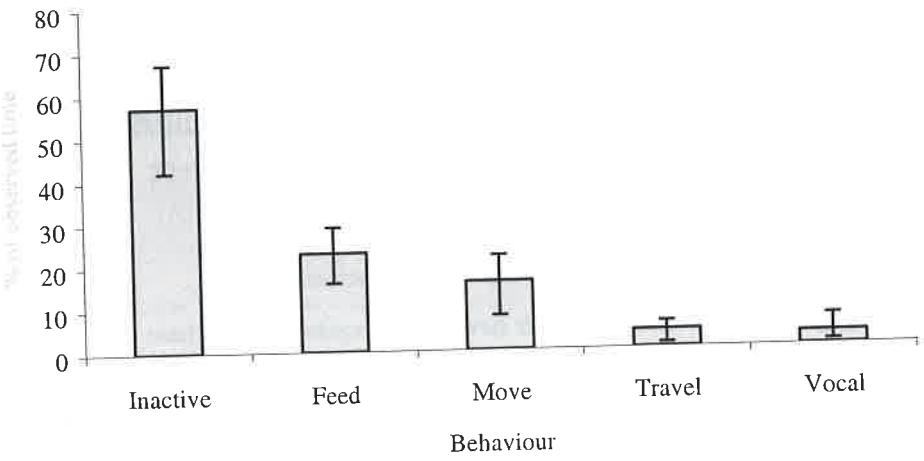

Figure 7. The percentage of observed time that porcupines were in engaged in different behaviour between 20:00-2:00 (n=7). Interquartile range is indicated as lines

Porcupines were inactive for over half the time they were observed (median 57%). During active time, the dominant activity across the night was feeding, which constituted a median 23% of observed time. Moving accounted for a median 16% of observed time, travelling 4% and vocalising only 3%.

Across hours of the night there was no significant difference in the percentage of time porcupines spent engaged in each behaviour (KW, Inactive: H=3.1, df=6, P=0.791; Feed: H=2.0, df=6, P=0.922; Move: H=5.0, df=6, P=0.549; Vocalise: H=4.0, df=6, P=0.719; Travel: H=3.2, df=6, P=0.779) (Figure 8). However within each hour there were significant differences in the representation of behaviours during 20:00 (KW, H=16.1, df=4, P=0.003), 21:00 (H=19.0, df=4, P=0.001), 23:00 (H=20.5, df=4, P<0.001), 0:00 (H=23.3, df=4, P<0.001), 1:00 (H=13.1, df=4, P=0.011) and 2:00 (H=11.0, df=4, P=0.028). During 22:00 there was no significant variation in the percentage time engaged in the different behaviours (H=3.9, df=4, P=0.424).

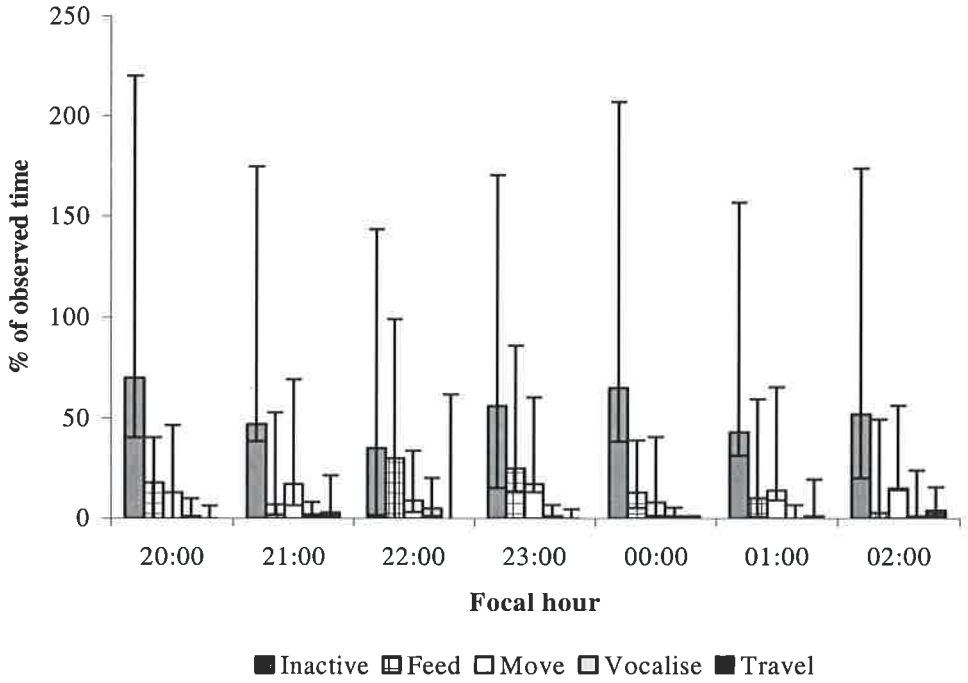

Figure 8. The median percentage of observed time that animals were engaged in different behaviour per hour between 20:00 to 2:00 (*n*=7). Interquartile ranges are indicated as lines.

Every hour of the focal night porcupines spent a greater percentage of time inactive than the combined percentages of other behaviours (median 52% of each hour). Of active behaviour, hours were dominated by feeding and moving behaviour (13% and 14% respectively). Porcupines were engaged in vocal behaviour for a negligible fraction of every hour (1%). Porcupines had a range of different vocalisations that were not frequently used. Three different vocalisations that were clearly identifiable were chattering (teeth chattering), buzzing (a deep, resonating sound) and whining (similar to a domestic dog). Due to low representation of travelling observations over all hours the median contribution of minutes travelling per hour was 0%.

4.3 Foraging behaviour

For the subsequent analysis of porcupine diet data from all focals (n=12) over maximum focal time (18:00–5:00) was pooled in an attempt to evaluate/accommodate the full dietary range.

4.3.1 Tree use by porcupines

Throughout each night porcupines were located on mean average in approximately 3 different 'tree stations' per night. Over the 12 focal nights animals were identified as using 6 different known species and two unknown species (where location of the focal porcupine could not be reliably pinpointed to one tree). White spruce (*Pi gl*) [1] accounted for 46% of all trees used (9 trees out of 35), trembling aspen (*Po tr*) 26%, and white cedar 15% (*Th oc*). To a lesser extent porcupines also used white birch (*Be pa*) (3% of trees), balsam fir (*Ab ba*) (3%), wild cherry (*Pr se*) (3%). The two unidentified species represented 3% each. All identified trees except the wild cherry were mature individuals, with a circumference >15 cm.

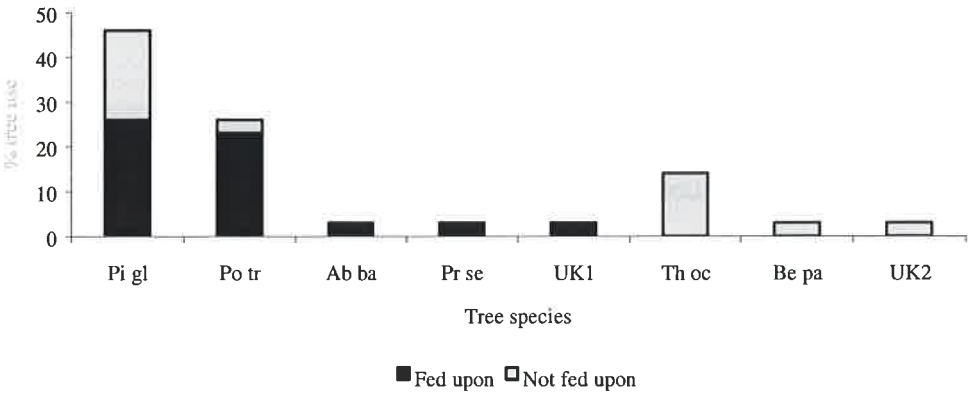

Figure 9. The percentage of trees used and not used by porcupines for feeding activity (n=12)

Porcupines were observed feeding in the canopy of 11 out of the 35 trees in which animals were seen (Figure 9). However, not all tree species were fed upon. White spruce and trembling aspen were the only two species in which animals targeted trees on separate occasions both to feed in, and not to feed upon. In trees where feeding activity was not observed porcupines were recorded inactive and (or) engaged in other non-feeding

[1] Latin names of trees mentioned in the text: Balsam Fir *Abies balsamea*, Trembling Aspen *Poplus tremuloides*, White Birch *Betula papyrifera*, White Cedar *Thuya occidentalis*, White Spruce *Picea glauca* and Wild Cherry *Prunus serotina*.

behaviour. Porcupines in balsam fir and wild cherry were observed to use these trees solely for feeding, whilst white cedar and white birch were used exclusively for other purposes.

Table 12. The number of trees fed and unfed upon of conifer and deciduous species

Number of trees	Tree Species	
	Conifer	Deciduous
Fed upon	10	9
Not fed upon	12	2

There was a significant difference between tree use and broad category of tree type (i.e. 'deciduous' and 'coniferous') (χ^2=4.0, df=1, P=0.046) (Table 12). Porcupines were recorded browsing on foliage in both coniferous and deciduous types of tree almost equally (10 conifers fed upon by animals and 9 deciduous). However, a greater number of animals were observed to be using deciduous trees for feeding purposes (9 fed upon) rather than residing in the trees and not foraging (two not used for feeding). Coniferous trees appeared to be used for foraging/not foraging purposes almost equally, although there is a weak suggestion that conifers may have been preferably not fed upon (10 conifers fed upon and 12 not fed upon). There was insufficient data to investigate porcupine feeding preferences between individual tree species.

Porcupines spent considerable amounts of time in trees, whether feeding or not feeding. Of tree species most frequently used, the median amount of time that animals spent in a single white spruce was 88 minutes, which represents 16% of median focal length of 542 minutes (n=10), and 119 minutes in a trembling aspen (22%) (n=8). From these estimations, if an animal were to target aspen trees the proposed mean of three trees in one night for the maximum median amount of time, an animal could be spending up to 86% of the focal night in arboreal locations alone.

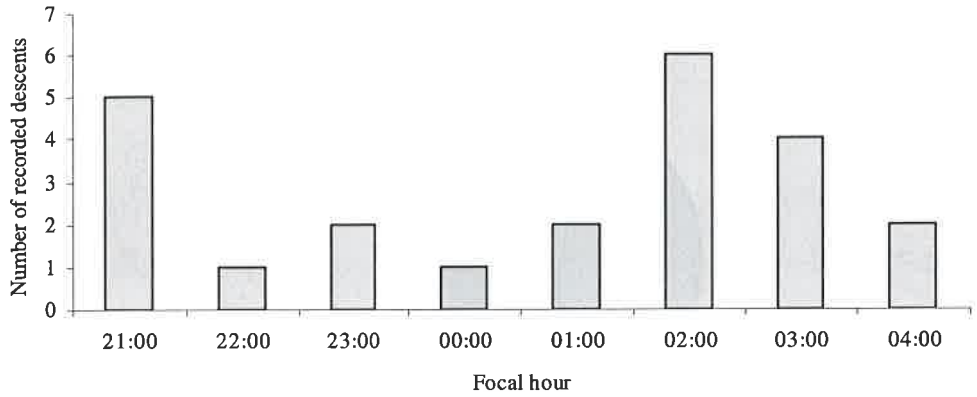

Figure 10. Number of recorded tree descents over hours of the focal night (n=23)

There was a significant association between hour and the number of tree descents recorded within that hour (χ^2 =8.7, DF=7, CV=14.07). Figure 10 illustrates a bipolar distribution of tree descents over the whole focal night (18:00-5:00). 22% of all recorded descents occurred during 21:00, (2-3 hours after the start of the focal) and 48% occurred during hours 2:00 and 3:00, (towards the end of the focal night). Between locating porcupines in their new tree stations, considerable focal time was spent engaged in the intervening radio-telemetry searches. Mean average telemetry search time between an animal descending its tree and leaving the observers vicinity and being re-located in a new (tree) location was 73 minutes (n=21).

4.3.2 Dietary breadth and tree foraging preferences

Porcupines were largely arboreal and folivorous in their feeding habits. Feeding activity took place in trees the majority of observed feeding time. For 66% of all focal observations feeding activity was exclusively arboreal (658 minutes of feeding, during eight out of the 12 focals). For 33% of focals porcupines fed both on tree foliage and ground vegetation (73 minutes feeding in trees, 91 minutes feeding on ground vegetation, during 3 of the 12 focals). Overall, tree feeding represented 89% of all feeding time recorded (731 minutes of 822 total minutes).

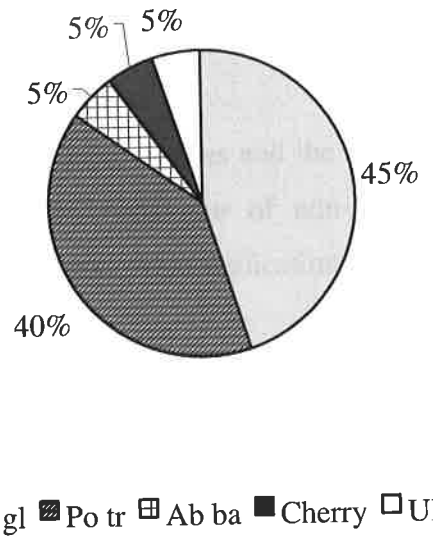

Figure 11. The percentage of different tree species in which porcupines were observed to feed (n=12)

Consumption of tree foliage (leaves from deciduous species, needles from coniferous) took place in 56% of all trees occupied by porcupines. Feeding activity was observed in five species: white spruce, trembling aspen, balsam fir, cherry and one unknown species (Figure 11). It appears white spruce and trembling aspen were most commonly fed upon. Of the 20 trees in which feeding took place 45% were white spruce, 40% trembling aspen, 5% wild cherry and 5% unknown. Small sample sizes prevented the application of a statistical test to these values, or calculation of a species diversity index.

4.3.3 The contribution of other plants to dietary breadth

When not located in trees, the remaining 11% of recorded feeding time (91 minutes of 822 minutes, during 3 out of the 12 focals) porcupines were observed foraging on three alternative ground vegetation types over six recorded feeding bouts. Grass (in meadow location adjacent to woodland) was consumed on three occasions, raspberry (Family *Rosaceae*) stems (in meadow/clearing) twice, and unidentified woodland edge non-woody vegetation once. The contribution of alternative forage to the observed diet was not sufficiently extensive to merit statistical analysis.

5 Discussion

General considerations

Only two replicates (focals) in five porcupines and the absence of replication in two may have resulted in bias towards the behaviour of non-replicated individuals and under representation of behaviour in others. More replication would have been desirable to test hypotheses with increased confidence.

Defining the most appropriate time of day at which to observe is an important practical issue of any study (Martin & Bateson, 1995). Because focal start time was inconsistent between focals and during the second part of the night animals were moving between trees and therefore difficult to locate, the amount of reliable/useful data on porcupine behaviour was reduced from 12 to 7 hours after data had been collected and summarised. Clearly to collect hours of data and then upon further analysis disregard much of them was not a practical use of fieldwork time. Continuous observations are labour-intensive yet generate substantial quantities of data over a short time. It could have been recognised by preliminary analysis of (pilot) data that a shorter focal period may not have compromised the quality of data collected.

Continuous sampling allowed every minute of observed behaviour to be recorded. The disadvantage of this was that decisions over identifying ambiguous behaviours had to be made fast, which may have contributed to recording error. However, to replace continuous recording with point sampling at intervals (*i.e.* every 5 minutes) rare behaviours (such as vocalisations) could have been missed.

The focal night was sectioned into hourly blocks for analysis because long periods of feeding and inactivity were recognised during pilot studies to be important components of porcupine nightly activity. By crudely dividing the night into hours the temporal distribution of short, rare behaviours (such as vocalisations) may have been poorly represented. It should also be recognised that behaviours may overlap the temporal divides (*i.e.* feeding behaviour starting at 20:00 and continuing into 21:00), thus one hours measurement may not have been independent of the next. Measuring average bout duration of behaviour in response to hour would have identified temporal variation and the extent of behaviour more accurately.

Specifically adult female porcupines were studied to eliminate gender-related and reduce age-related variability between animals. However, the effect of season was not measured and may have influenced behaviour where focals were widely spaced throughout the study period. In particular, reproductive status and general condition of focal animals may have altered considerably between May and July.

Methods used to record data were biased towards audible means. Foliage often obscured direct visual observations of porcupines and radio-telemetry use was reserved for when animals were out of sight or sound but a check on activity needed to be made. Visual observations were made wherever possible when there was unrestricted view of the animal either on the ground (*i.e.* foraging in meadows) or in the branches of trees. There may have been biases towards seeing porcupines in deciduous trees versus conifers due to tree architecture where the branches of deciduous trees were more widely spaced therefore a porcupine was much easier to see.

It is misleading to assume that in all situations visual methods always provided the most accurate method of recording behaviour as relying on visual recording methods alone may have resulted in under-recording behaviours only detectable by ear. The clearest view of animals in trees was frequently from a rock outcrop parallel to the animal in its tree, distanced 5-10 m from the tree. From such distance vocalisations may have been inaudible to the observer and if the visible animal moved out of sight it was hard to hear signs of movement. Audible methods in synchrony with visual observations at a close distance would provide the best methodology for future study although this may not always prove practicable. Due to restrictions of working in the dark it may also be advisable to limit the categories of behaviour investigated so that ambiguity surrounding some categories may be reduced.

Nocturnal activity patterns: preliminary analysis

Preliminary analysis served a useful purpose in exploring the data and defining which period of the night further analyses should be carried out. Significant differences between porcupines in observation time and in the extent that they were active within observation time means conclusions must be drawn cautiously.

Most observations describe arboreal behaviour in porcupines. For practical reasons once an animal had been successfully located during a focal it was relatively easy to maintain

contact with her for several hours whilst she remained in the same tree. Observing terrestrial behaviour was rare because dense forest vegetation often prevented the observer locating and approaching a porcupine on the ground. However whilst in trees porcupines fed on tree foliage for the greatest proportion of their active time, for which a tree location was obviously essential. Hence observations of porcupines in trees may be an ecological function of porcupines being in trees anyway due to their major requirements for tree foliage.

The greatest number of porcupines observed for 30 minutes or more was between 20:00 and 2:00. Animals were located between 19:00 and 21:00 at the start of a focal night therefore as 20:00 is the central hour within this time it is not surprising that it was from this hour onwards that most animals were observed. Following 2:00 there was a fall in the number of animals observed for 30 minutes of more each hour. Most tree descents were recorded at 2:00 and 3:00. Therefore reduced number of porcupines observed after this hour may have been because the observer was involved in the ensuing radio-telemetry searches following a tree descent instead of engaged in porcupine observations. Radio telemetry searches lasted on average over an hour, therefore unobserved time following tree descents at this time may have had a considerable effect on the number of animals observed in the successive hour. It may have been convenient to have defined radio-telemetry time (the majority of unobserved time) as an additional behavioural category (*i.e.* 'travel between tree stations'), therefore most unobserved time could have been included as part of the activity budget. However, time that animals were unobserved was extensive and it could not be assumed that porcupines were solely travelling between descending a tree and being relocated in a new tree.

Activity budget for *Erethizon dorsatum*

An overview of behaviour over the condensed night revealed animals engaged in all behaviours for one minute or more throughout all hours of the night. Duration of behaviour could range from one to 60 minutes of an hour. Therefore this interpretation (similar to 'one-zero' sampling (Martin & Bateson, 1995)) served only to demonstrate whether or not a behaviour occurred during hours across the night. The limitations of this are that short bouts of behaviour (*i.e.* a single vocalisation lasting one second) were scored equally to long bouts (*i.e.* continuous feeding behaviour lasting 60 minutes) and the time periods between measurements were too broad to make valuable inferences. Such a

sampling technique may be useful in describing the incidence of specific rare behaviours that may otherwise be missed by continuous sampling methods.

Inactivity and moving were recorded frequently throughout the focal night. This may have been because both were broad categories of behaviour, encompassing other behaviours within them. For example, during 'inactivity' both resting and vigilance behaviour could not be distinguished between when only audible recording methods were used. Moving behaviour was hard to separate from travelling and feeding, as animals were obliged to move as they foraged on leaves.

The amount of time that porcupines were observed throughout hours of the night did not differ significantly between hours and time observed was significantly greater than time unobserved. Therefore time budgets were calculated from data assumed to be representative of behaviour occurring within the hour.

Inactivity

Inactivity was the most common behaviour observed throughout all hours. During inactive bouts vigilance, resting and digesting may have been taking place, and their occurrence may not have been mutually exclusive.

Time spent vigilant will contribute to the time budget of any animal under predation risk or those affected by the movements of conspecifics competing for shared resources. It is recognised that individuals of many species are more vigilant when solitary than when in groups, and this may extend to porcupines who are solitary throughout most of the year (Dehn, 1990). Conversely anti-predator strategies such as crypsis and mechanisms for self-defence that reduce predation detection and attack success may simultaneously reduce the need for vigilance behaviour. Crypsis and the use of body armour have been documented as important folivore adaptations in predator avoidance and escape (Eisenberg, 1978). Quills serve to protect the porcupine against most predators and brown/black pelage and quill coloration reduce its detection. As a result of its body protection and relatively inaccessible arboreal location the porcupine in a tree has few predators and time devoted to vigilance for predators may not be considerable. The fisher, *Martes pennanti* (Family *Mustilidae*) is the only predator documented able to attack porcupines in trees, by targeting the porcupines face as the animal carefully descends its tree backwards (Web-ref:1). To date, there has been no survey of fisher populations in

Parc du Bic, although remains of fisher-predated porcupines have been recovered (personal communication, J Roberge). Another potential (minor) porcupine predator also present in the park was the coyote *Canis latrans* (Roze, 1989).

In anecdotal observations porcupines were observed to pause at the base of their tree after a descent before travelling off. This pause may be preparation for ground travel that serves a useful purpose as porcupines leave the relative safety of the trees to travel. Slow locomotion before travelling on open ground has been related to predation pressure in the slender loris *Loris tardigradus*, a semi-folivorous small primate of India (Nekaris, 2001). Another explanation may be that the animal is spatially orientating itself before moving off, having spent considerable time in one tree and needing to recognise its position in the forest. It is unknown to what extent observer presence may have initiated this behaviour, as porcupines may have been able to detect the observer during the descent if the observer was very close. On more than one occasion during observation under infra-red a porcupine directly approached a observer positioned < 3 m from its tree and upon catching their scent quills were raised and the animal quickly retreated. The proximity of the observer may have caused periods of extended vigilance on other occasions *i.e.* in disturbing nearby habitat when searching for animals.

Predator avoidance tactics and a sedentary (*i.e.* largely inactive) lifestyle observed in porcupines may have evolved in response to associations between metabolic rate, arboreal lifestyle and dietary specialisation towards folivory. In general, anti-predator strategies such as crypsis and body armour have been predicted for animals of low BMR exhibiting habitat and dietary specialisation (Lovegrove, 2000), and more specifically for large arboreal folivores (McNab, 1978). The cryptically coloured folivorous three-toed sloth *Bradypus griseus* has a BMR 42% of that predicted from scaling metabolic rate with body mass and the folivorous prehensile tailed South American porcupine (*Coundou prehensilis*) has BMR 45% of that expected (McNab, 1978).

The basal rate of arboreal mammals has been estimated at 66% lower than terrestrial mammals, whilst folivores are predicted a BMR 71% lower than grazers and 62% that of frugivores (Arends & McNab, 2001). A BMR has been negatively correlated with the extent of arboreality and folivory in arboreal folivores in general (McNab, 1978, 1988) and more specifically in caviomorph rodents (New World hystricognaths), which includes the North American porcupine (Arends & McNab, 2001). The explanations for this may be true to porcupines in this study: low nutritional density of a primarily leaf diet which limits

energy intake, the arsenal of chemical and structural plant defences influencing energy gain, and the low muscle mass of large tree dwelling animals inhibiting energetic scope (in these mammals muscle mass < 33% of total mass is common and the corresponding low muscle to mass ratio is believed to reduce energetic expenditure (McNab, 1978). Therefore it may be postulated that porcupines should exhibit a reduced BMR compared to other herbivorous mammals of similar mass due its mass, dietary specialisation towards mainly tree leaves and its semi-arboreal nature.

If porcupines do exhibit a low BMR this may affect their ability to thermoregulate, as has been observed in many folivorous marsupials (McNab, 1978). A reduced ability to control body temperature and sedentary lifestyle may increase reliance on external insulation (considered important in enabling three-toed sloths to maintain thermal neutrality (Nagy & Montgomery, 1980)). Behavioural responses that may increase inactivity as a result of poor thermoregulation include huddling (in cold conditions), basking (in warm conditions) and using nests and shelter (Frey, 1991). Although porcupines do not hibernate during the cold winter, animals have been observed to increase their social interactions beyond the breeding season by sharing communal den-sites during cold winter months (Roze, 1989) in contrast with occasional solitary den use observed throughout the rest of the year (Roze, 1986). It has not been identified whether this is a direct behavioural response to maintain warmth at reduced metabolic cost, whether it is due to limited den sites or serves a more socially complex function. South western Québec annual temperatures may range from -36°C to + 36°C (web-site ref:2) and whether den sharing in relation to temperature occurs in the Parc du Bic porcupines and the social and biological implications of this could be a focus for future studies.

Conversely an advantage that porcupines and other arboreal folivores may gain from a relatively inactive lifestyle and low BMR is that consequently their reduced energetic demands may be maintained at little energetic cost (Cork & Foley, 1997). To achieve this porcupines may have to choose foliage carefully and moderate activities so not to waste energy. Some arboreal folivores such as the Madagascan grey mouse lemurs *Microcebus murinus* may enter torpor for several hours during periods of food shortage and cool temperature, which is believed to be a strategy to conserve energy and water (Schmid & Speakman, 2000). Although torpor has not been observed in porcupines, during winter months activity may decrease and may serve a similar function (Roze, 1989).

Contributing to the large proportion of time porcupines were recorded inactive will be time spent resting (*i.e.* asleep or immobile). Resting bouts throughout the night may be an inevitable consequence of the digestive constraints imposed by herbivory. Although initial handling time in gathering and ingesting foliage may be short because leaves (in particular conifer needles) may be easily consumed and are available in the canopy at high biomass density, the subsequent fermentation of ingested plant components by micro-organisms in the porcupines caecum is generally believed to be a slow process (Roze, 1989), increasing overall handling time. As the gut can only contain a maximal volume of food a digestive bottleneck' may result whereby food ingestion may slow or cease so that food already ingested may be processed. This may demonstrate the typical Type II functional response observed in herbivores feeding in patches where food items are concentrated in space and where handling time constraints eventually limit food (prey) intake rate irrespective of food density, (Begon *et al.*, 1990; Gross *et al.*, 1993).

Porcupines are not unique in the large proportion of time they were inactive as long periods of inactivity have been observed in other arboreal, folivorous species. The 57% inactive time observed in porcupines may be tentatively compared with 84% inactivity in the folivorous tree hyrax *Dendrohyrax arboreus,* an arboreal rodent (1-5 kg mass) from the tropical montane forest of central Africa (Milner & Harris, 1999) and 80% inactivity in the leaf-eating bear cuscus *Ailurops ursinus* a 7 kg arboreal marsupial, from lowland tropical forest habitat (Dwiyaherni *et al.,* 1999). However comparisons between species across taxonomic divides and from widely different ecosystems must be drawn cautiously. Meaningful comparisons need extensive information on differences between feeding strategies, body mass and gut size and degree of gut specialisation. Bioenergetic considerations and social behaviour should also be included.

Feeding

Feeding behaviour was the most common active behaviour observed in porcupines. Porcupines fed almost equally upon leaves of white spruce *Picea glauca* and trembling aspen *Poplus tremuloides* and showed only a marginally significant difference between feeding use of broad groups of conifer and deciduous species in general. This did not correlate with previous studies that stress preferences for deciduous trees during the summer growing season and conifers (for bark and needles) during winter months (Roze, 1984, 1989; Synder & Linhart, 1997;). Specifically, white spruce has not been documented as a summer food item, although its bark has been considered an important

winter food in one study (Murie, 1926). It may be that due to small sample sizes and combined data for all focals biased results were produced. However, as this is the first study of porcupine activity in the study area (or mixed forest of south west Quebec) it is important to repeat and extend this study before rejecting the observations made.

Leaves from evergreen and deciduous plants differ in chemical composition in terms of nutrient quality (Janzen, 1978; Archibold, 1995) and concentrations of plant secondary metabolites (Prudhomme, 1983). Broadly speaking, nutrient concentrations are higher in the trunks and branches of deciduous species than conifers but the nutrient content of conifer needles is higher than that of deciduous leaves. In addition the needles of conifer are year-round sites of nutrient accumulation and storage, whilst deciduous leaves experience wide seasonal fluctuations in their chemistry (Archibold, 1995). In consuming foliage from both species a porcupine may profit from the high nutrient quality in deciduous leaves whilst conifer needles, although less nutritious, provide a more predictable nutrient source. Needles are small, compact and numerous along branches whilst deciduous leaves are generally larger and more widely distributed. Porcupines may be able to compensate for the comparative nutrient deficiency in needles by being able to consume larger quantities of needles than leaves per unit time.

Although it has long been considered that animals preferentially seek food of high energy content to obtain an optimal diet, (*i.e.* energy maximisation/foraging effort) (Stephens & Krebs, 1986), it appears that plant chemical and structural defences may be the major determinant of food choice in herbivores (Bryant & Kuropat, 1980; Coley *et al.*, 1985). Although measuring plant secondary metabolite (PSM) concentrations of potential food items available to porcupines was beyond the scope of this study, general differences in concentration of PSM's between conifers and deciduous trees may have strongly influenced porcupine food choice (Prudhomme, 1983). It is recognised that trees with long leaf longevity and slow growth rates, such as conifers, accumulate more defensive chemicals than deciduous, fast growing trees (Palo & Robbins, 1991). White cedar *Thuya occidentalis* was used extensively but porcupines were never observed to feed upon cedar needles. The physiological tolerance threshold for the PSM's occurring in cedar may have been lower than the tolerance for PSM's in spruce.

Trees not used for feeding (such as white cedar) may have been selected for their structure to serve a useful alternative purpose as high quality shelter. As porcupines use dens only occasionally (Roze, 1989) and spend most time inactive and exposed to the elements in an

elevated arboreal location, choosing the appropriate tree in which to shelter when not foraging may be of paramount importance. Differential use of trees has been observed in porcupines in Texas Pinyon (*Pinus remota*) - Juniper woodland where some trees were used as resting sites and bark feeding and others were used for resting and foliage consumption (Ilse & Hellgren, 2001). It has been recognised that porcupines may demonstrate fidelity to trees for both foraging and resting use (Curtis, 1944; Roze, 1989). Porcupines in Parc du Bic may do this and whether trees are chosen for feeding or shelter on the basis of leaf nutrients or the suitability as a shelter refuge could be considered in future work.

Ground vegetation did not feature greatly in porcupine diet, and this could be a feature of the bias towards arboreal observations. However, it may be that the porcupine's arboreal adaptations reduce any potential advantages of feeding on the ground. Terrestrial feeding may lose its importance to porcupines as summer progresses and tree leaves emerge. Porcupines have been reported feeding on raspberry stems in late spring in other studies because trees come into leaf later than ground vegetation starts to grow (Roze, 1989). In accordance, the observation of raspberry feeding in this study was for one animal in May.

By this study porcupines may be considered feeding specialists, rare in herbivores generally but observed in some folivores (Cork & Foley, 1997; Dearing *et al.*, 2000). There is evidence that feeding on a narrow range of plants results in excessively high concentrations of a limited range of plant secondary metabolites (PSM's) that mammalian detoxification pathways are considered incapable of removing (Dearing *et al.*, 2000). Porcupines are normally considered generalists (Roze, 1989) and the observed narrow dietary breadth in this study may have been a direct consequence of limited data. However, seasonal selectivity has been observed in porcupines and may be related to the seasonal availability of forage influencing food choice (Snydar & Linhart, 1997).

Laboratory studies have identified porcupines as highly efficient in extracting energy and protein from fibrous, tannin rich forage. Indeed they have superior fibre digestion capabilities compared to other hind gut fermentors and some ruminants (Felicetti *et al.*, 2000) and it is believed they have exceedingly low nitrogen requirements compared to other eutherians (Fournier & Thomas, 1997). This enables them to subsist on a comparatively poor quality diet such as tannin-rich leaves and may offer them flexibility in their diet choice as nitrogen is one requirement often limiting in herbivore diets that may not be in porcupine diets (Palo & Robbins, 1991). In addition, the porcupine's large distal

colon may increase the capacity for water and electrolyte resorption increasing the scope for porcupines to forage on fibrous foliage. Importantly the caecum of porcupines may serve as a sodium (Na) store (Vispo & Hume, 1995), which may serve useful purpose as seasonal sodium imbalance due to changes in plant chemistry may modify herbivore behaviour, and has been suggested to be a limiting factor in herbivore populations (Weeks & Kilpatrick, 1976; Belovsky & Jordan (1981).

An ability to feed intensively on plants that are locally very abundant yet high in PSM's may reduce browsing competition on that tree by other herbivores. However it is unknown whether porcupines were feeding on trees in relation to their abundance within the individuals home range (and over the whole study area, as home ranges may overlap and animals are capable of travelling within adjacent home ranges), or as a consequence of PSM concentrations for which porcupines may have developed aversion.

Porcupines must be able to assess forage quality before deciding to ingest considerable quantities, then self-regulate their intake and adapt feeding choice as a functional response to feedback mechanisms. Prior experience of feeding in particular trees may influence feeding tree choice as well as immediate signals from leaf palatability. It has been hypothesised that young three-toed sloths (and perhaps Atlantic forest maned sloths *Bradypus torquatus*) learn which plant species to consume from their mothers (Chialerro, 1998). The same may be true of porcupines, as the single offspring may remain closely associated and foraging with its mother for up to four months post birth (Roze, 1989).

Animals may detect PSM concentrations in plant parts through odour not detectable by humans and may instinctively recognise or learn to avoid them (Provenza *et al.,* 1990). Both koalas and ring-tailed possums *Pseudocheirus* spp. and *Hemibelideus lemuroides* have been observed to smell leaves carefully before ingestion and gently shaking a branch may be sufficient to release volatile PSMs such as terpenoids (Lawler *et al*, 1998). Porcupines have been observed to carefully examine twigs with leaf buds on by scent, bending them within reach of their mouth before feeding (Murie, 1926). Upon sampling the PSMs in leaves mammals can learn to associate distinctive flavours with the presence of PSMs, and may learn to control intake from nausea or gastro-intestinal illness.

Within any chosen feeding tree subtle differences between leaf quality at different canopy levels and along specific branches may have affected porcupine decision-making and were not assessed by this study. Although assumed that needles and leaves were chosen,

differences in specific plant parts that were chosen within the tree canopy which may have been overlooked, and may have varied in relation to plant chemistry (Wrangham & Waterman, 1981). How animals were observed to be selecting individual food items and estimations of bite-sizes were not recorded (largely because such detail could rarely be seen). Both are factors that could influence feeding activity and could be used in further quantification of foraging choice (Gross *et al.*, 1993).

Individual preferences may not represent diet breadth in the population as a whole. During winter months individual porcupines in the north east States have been observed to feed on 1 to 2 tree species, whilst the general population was feeding on at least 8 tree species (Roze, 1984). This may be because there are factors influencing food choice at the level of the individual that may not be apparent at the level of the population (such as home range restrictions on forage availability and individual sensitivity to PSM's).

Other arboreal species that consume foliage to some degree in their diet have been observed to spend considerable amounts of active time feeding. The 23% observed time spent feeding by porcupines may be compared an with an average of 11% of time spent feeding by tree hyrax, an selective herbivorous broswer with a similar hind-gut fermentation specialisation and considered a selective folivorous browser (Gaylard & Kerley, 1997). The mahogany glider, a frugivorous marsupial, is reported to spend over 60% of its time foraging and in travel related to foraging (Jackson & Johnson, 2002). Wild chimpanzees, tree-dwelling omnivores, may spend up to 30% of their time activity feeding (Matsumoto-Oda & Oda, 1998).

Moving

Moving behaviour was frequently documented in porcupines and included scratching, sniffing, shaking and re-orientation on branches.

The contribution of scratching and shaking moving behaviour may have been related to temperature and the abundance and activity of biting insects. Harassment by mosquito *Aedes* spp. and black-fly *Simulium* and *Prosimulium* spp. may have initiated a behavioural response in porcupines that affected their activity pattern. The seasonal influence of temperature and mosquito abundance affects the activity budget of caribou *Rangifer tarandus* so that during warm weather during heavy insect harassment they spend more time moving at the expense of foraging time (Mörchschel & Klein, 1997). Although an

index of insect harassment on the observer was periodically recorded (for purposes not considered in this study) associations between temperature, level of insect harassment and incidence of scratching and shaking porcupine behaviour were not tested because these behaviours were comparatively rare over the whole night.

Vocalising

In conjunction with using crypsis as a predator avoidance strategy animals may also reduce predator detection by not forming cohesive social groups and reducing the vocalisations they use to a specific repertoire. In contrast, frequent vocalisations may function in territorial defence (Jackson and Johnson, 2002).

It has been proposed that infrequent use of vocalisations and the almost complete absence of responses to calls is related to the lack of social interactions observed between mahogany gliders *Petaurus gracilis* (excudivorous 400 g marsupials). This may extend to porcupines as they spent very little time vocalising and are solitary most of the year and generally non-territorial (Roze, 1989). It may be that porcupine vocalisations serve primarily as a warning signal (Roze, 1989) and it was noted that a short series of chattering vocalisations frequently preceded a tree descent by a few minutes although this interaction was not fully investigated and tested. Such signalling may serve as a threat warning to conspecifics and other animals., and observer presence could not be discounted as a cause.

There may be marked seasonal variation in vocalisations as they serve a social function in interactions between and within the sexes during the reproductive season. This has been observed in porcupines whereby increased vocalisations related to breeding activities begin in late August and may continue throughout the winter (Ilse & Hellgren, 2001).

Travelling

It should be recognised that because ground travel was rarely seen and porcupines did not travel extensively whilst in trees the extent of time porcupines travel was probably under-represented in this study.

Porcupines were considered to be travelling when they could be seen or heard climbing (*i.e.* sound of claws on bark) amongst tree branches or on the tree trunk during a descent. Generally, movement and travel of porcupines was slow and deliberate on the ground and amongst tree branches. When animals were feeding they usually remained on the same

branch for long periods, seemingly systematically depleting the immediately available leaf biomass. Therefore they did not appear to spend considerable time climbing and travelling within trees.

Much travelling activity was assigned to tree descents when the focal porcupine could be clearly heard or seen. It may be that during tree descents porcupines are at their most vulnerable as they descend backwards, body closely hugging the tree trunk and vision may be restricted for several minutes during the descent. This may have been why animals descended trees quickly, and may contribute to why travel time was poorly represented.

In prairie voles *Microtus ochrogaster*, the digestive bottleneck effect already discussed is believed to limit food intake and keep feeding bouts spaced, and may be an explanation for their 2-4 hour activity rhythm (Zynel & Wunder, 2002). Such an effect may be contributing to the median four-hour periodicity observed between tree descents in porcupines.

6 Summary and future work

This study demonstrated how porcupines can be studied in their natural habitat to provide quantitative estimates about how individuals may partition their time. A review of the methodology identified some of the potential sources that may contribute to error in future behavioural work on porcupines, and generated some recommendations as to how improvements could be made.

The porcupines spent most of their night inactive, with active time spent predominantly feeding and moving, and very little time engaged in other behaviours such as vocalising and travelling. A combination of body form (including gut size and degree of specialisation), metabolism, social behaviour and physiological adaptations may influence how porcupines partition their time.

It can be identified from the activity budget that porcupines primarily occupy an arboreal niche, with great reliance on a few tree species for food. It is not known which factors are most important in influencing feeding preferences in porcupines for particular tree species. A habitat assessment would be useful so that tree preferences observed in porcupines can be related to abundance and availability of the tree species present.

A natural extension of this pilot study would be identify and quantify the species of secondary compound and nutrients present in different foliage. Energetic expenditure of wild porcupines could be calculated by doubly labelled water techniques and this related to leaf energy value for different plant species. Canteen food choice experiments on captive porcupines would compliment repeating behavioural observations on wild animals.

An extensive comparative review of activity budgets would place further work on North American porcupines into the wider context of other arboreal folivores. Comparisons of time budgets within and between taxonomic groups should include information on geographical location, metabolic differences and diet. To elucidate why porcupines are unique in their temporal arboreal niche, any review should focus on animals occupying the fringes of temperate ecosystems.

This study was useful in setting the scene for future behaviour work on porcupines at Parc du Bic. It is anticipated that a long-term future of research in the park may generate further unique opportunities to improve the understanding of porcupine ecology.

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Appendix I: Maps

Map 1
The geographical distribution of *Erethizon dorsatum* throughout the United States and Canada

Source:
www.washington.edu/burkemuseum/ mammalogy/erdo.html

Map 2
The location of the Parc du Bic National Park within the province of Quebec, Canada

Source:
http://www.mapquest.co.uk/cgibin/ia_find?link=school/worldatlas_index&uid=u0lelbiesciayfhc:ynuz8w167&atlas=quebec

Map 3
Parc du Bic within the Bas St. Lawrence, Quebec, Canada

Source:
http://www.parcdubic.com/PicP1BF/p07.htm

Appendix II: Tables

Table 2. Biometric data collected from porcupines captured on the study area of Parc du Bic National Park, Quebec. Measurements were taken from 2002 capture data as follows: Body mass – weight was recorded using a 100g spring balance (Pesola AG, Baar, Switzerland); Body length – base of the nose to the tip of the tail; Mean chest width – width of the ventral surface of the animal, between the front legs; Hind foot length and breadth – surface of the foot pad at longest and broadest point. Note: All measurements were taken whilst the animals were under sedation and therefore in muscular relaxation. Data describes actual values or means from multiple captures with corresponding standard deviations in parentheses.

Focal individual	Date of first capture	Mean body mass (kg)	Mean body length (cm)	Mean chest width (cm)	Mean hindfoot length (cm)
A	July-00	6.0 (0.44)	71 (-)	49.5 (-)	6.3 (-)
B	May-00	7.8 (0.67)	72 (0.35)	54 (7.07)	6.6 (-)
C	May-00	6.5 (0.6)	72 (0.45)	56.7 (3.51)	6.4 (2.65)
D	May-00	5.6 (-)	-	-	-
E	May-01	8.7 (0.59)	74 (-)	50 (-)	6.3 (-)
F	May-00	5.7 (0.71)	69 (-)	51 (-)	6.0 (-)
G	June-00	6.9 (0.52)	74 (-)	49 (-)	6.3 (-)
Mean (SD)		6.7 (1.15)	72 (1.9)	51.7 (3.03)	6.3 (0.19)

Table 2. Mean observed (active and inactive) and unobserved focal time (minutes) for each focal porcupine (animals labelled A-G) and medians of all animals

Focal Porcupine	Time observed (mins.)			Time unobserved (mins.)	Total focal length (Time observed + time unobserved)
	Active	Inactive	Σ		
A	163	253	416	143	559
B	162	197	359	183	542
C	206	107	313	263	576
D	114	235	349	156	505
E	130	91	221	320	541
F	84	217	301	184	485
G	141	227	368	224	592
Median	141	217	349	184	542
% of median total focal length*	26	40	64	34	

* the use of medians may generate approximate percentages

Table 3. Number of minutes porcupines were observed in tree, ground and unknown locations during total observed time for all focals (1796 minutes) (n=12)

Observed time (minutes)	Location		
	Tree	Ground	Unknown
Total	**1528**	**260**	**8**
%	85.1	14.5	0.4

Table 4. The number of porcupines engaged in one or more minutes of active behaviour during hours throughout the focal night (18:00-05:00) (n=12)

	Focal hour											
	18:00	19:00	20:00	21:00	22:00	23:00	0:00	1:00	2:00	3:00	4:00	5:00
n porcupines active*	1	5	11	12	10	12	11	11	11	7	4	2
% of all animals	8	42	92	100	83	100	92	92	92	58	33	17

*active for one minute or more within the hour

Table 5. Hours of the focal night during which focal animals were observed (active or inactive) more than 30 minutes, and the number of animals for which observations were recorded (n=12)

	Focal hour											
	18:00	19:00	20:00	21:00	22:00	23:00	0:00	1:00	2:00	3:00	4:00	5:00
n porcupines observed*	0	2	8	8	7	8	10	9	9	2	5	1
% of all animals	0	17	67	67	58	67	83	75	75	17	42	8

*observed (active or inactive) for 30 minutes or more within the hour

Table 6. The number of minutes that different methods were used in recording data on each porcupine during observation time between 20:00 and 2:00 (n=7)

Minutes per animal	Method		
	Telemetry	Visual	Audible
A	13	179	81
B	22	78	156
C	1	95	274
D	2	2	105
E	13	63	162
F	10	7	61
G	12	35	189
Median	12	63	156
% of observation time	5	28	68

Table 7. The percentage of porcupines engaged in different behaviour between hours 20:00-2:00 (n=7)

%	Focal hour							Median
porcupines	20:00	21:00	22:00	23:00	0:00	1:00	2:00	
Inactive	79	93	64	100	100	79	93	93
Moving	64	100	57	100	86	93	86	86
Feeding	57	57	57	79	79	64	36	57
Vocalising	43	57	50	43	43	36	43	43
Travelling	29	43	29	29	14	36	50	29

*active for one minute or more within the hour

Table 8. The percentage of time (minutes) that porcupines were observed and unobserved during all hours between 20:00-2:00 (n=7)

% of time (minutes)	Focal hour							
	20:00	21:00	22:00	23:00	0:00	1:00	2:00	Median
Observed	69	74	58	65	86	86	60	69
Unobserved	31	26	43	35	14	14	40	31

Table 9. The median number of minutes per focal that porcupines were in engaged in different behaviour between 20:00-2:00 as a proportion of time observed (n=7)

Behaviour	% of observed focal	Interquartile Range (mins.)	
		Q1	Q2
Inactive	57	42	67
Feed	23	16	29
Move	16	8	22
Travel	4	1	6
Vocal	3	1	7

Table 10. The median percentage of observed time that animals were engaged in different behaviour per hour between 20:00 to 2:00 (n=7)

% of observed time	Focal hour							
	20:00	21:00	22:00	23:00	0:00	1:00	2:00	Median
Inactive	70	47	50	56	65	43	52	52
Feed	18	6	24	25	13	10	3	13
Move	13	17	9	17	8	14	15	14
Vocalise	1	2	5	1	1	0	1	1
Travel	0	3	0	0	0	1	4	0

Corresponding interquartile ranges plotted IQ	Focal hour						
	20	21	22	23	0	1	2
IQ1	29.60	8.46	33.31	40.83	26.70	11.63	31.94
IQ2	150.10	127.80	108.51	114.47	142.14	113.63	121.84
IQ1	18.33	5.23	30.23	11.45	7.71	9.45	2.83
IQ2	22.37	45.83	69.13	60.80	25.82	49.45	46.45
IQ1	13.17	10.55	5.70	3.97	6.67	4.94	0.74

Table 11. The number of different trees used and not used by porcupines for feeding activity during all focal time

Number of trees (and % of all trees)	Tree species															
	Pi gl		*Po tr*		*Ab ba*		*Pr se*		*UK1*		*Th oc*		*Be pa*		*UK2*	
Tree fed upon	9	(26%)	8	(23%)	1	(3%)	1	(3%)	1	(3%)	0	(0%)	0	(0%)	0	(0%)
Tree not fed upon	7	(20%)	1	(3%)	0	(0%)	0	(0%)	0	(0%)	5	(14%)	1	(3%)	1	(3%)
Total	16	(46%)	9	(26%)	1	(3%)	1	(3%)	1	(3%)	15	(14%)	1	(3%)	1	(3%)

Table 12. The number of trees fed and unfed upon of conifer and deciduous species

Number of trees	Tree Species	
	Conifer	Deciduous
Fed upon	10	9
Not fed upon	12	2

Table 13. Number of tree descents over hours of the focal night (n=23)

hour	Focal hour							
	21:00	22:00	23:00	00:00	01:00	02:00	03:00	04:00
Number of recorded descents	5	1	2	1	2	6	4	2

Table 14. The species and number of trees that porcupines were observed feeding upon during all focal time

	Tree species				
	Pi gl	***Po tr***	***Ab ba***	***Pr se***	***UK1***
# trees fed upon by porcupines	9	8	1	1	1
% of all trees	45	40	5	5	5

Appendix III: Statistical tests

Nocturnal activity patterns: preliminary analysis

An overview: the extent that porcupine behaviour was observed during the focal night

Source: Table 2, Figure 1

Chi-Square Test: Unobs, Obs

Expected counts are printed below observed counts

	Unobs	Obs	Total
1	286	831	1117
	440.07	676.93	
2	365	716	1081
	425.89	655.11	
3	526	626	1152
	453.86	698.14	
4	156	349	505
	198.96	306.04	
5	639	444	1083
	426.68	656.32	
6	184	301	485
	191.08	293.92	
7	447	737	1184
	466.47	717.53	
Total	2603	4004	6607

```
Chi-Sq = 53.941 + 35.067 +
          8.705 +  5.659 +
         11.466 +  7.454 +
          9.275 +  6.030 +
        105.657 + 68.688 +
          0.262 +  0.170 +
          0.812 +  0.528 = 313.717
DF = 6, P-Value = 0.000
```

Chi-Square Test: Active, Inactive

Expected counts are printed below observed counts

	Active	Inactive	Total
1	325	506	831
	373.78	457.22	
2	323	393	716
	322.06	393.94	
3	412	214	626
	281.57	344.43	
4	114	235	349
	156.98	192.02	
5	261	183	444
	199.71	244.29	

6	84	217	301
	135.39	165.61	
7	282	455	737
	331.50	405.50	
Total	1801	2203	4004

Chi-Sq = 6.367 + 5.205 +
0.003 + 0.002 +
60.413 + 49.389 +
11.768 + 9.620 +
18.809 + 15.377 +
19.506 + 15.947 +
7.392 + 6.043 = 225.840
DF = 6, P-Value = 0.000

Hours of the night during which most observations on behaviour were recorded

Source: Table 5, Figure 3

Between 18:00-5:00

Chi-Square Test: NO. PORCS OBS/30, NO.PORCS UNOBS

Expected counts are printed below observed counts

	NO. PORC	NO.PORCS	Total
1	0	12	12
	5.75	6.25	
2	2	10	12
	5.75	6.25	
3	8	4	12
	5.75	6.25	
4	8	4	12
	5.75	6.25	
5	7	5	12
	5.75	6.25	
6	8	4	12
	5.75	6.25	
7	10	2	12
	5.75	6.25	
8	9	3	12
	5.75	6.25	
9	9	3	12
	5.75	6.25	
10	2	10	12
	5.75	6.25	
11	5	7	12
	5.75	6.25	
12	1	11	12
	5.75	6.25	
Total	69	75	144

```
Chi-Sq =  5.750 +  5.290 +
          2.446 +  2.250 +
          0.880 +  0.810 +
          0.880 +  0.810 +
          0.272 +  0.250 +
          0.880 +  0.810 +
          3.141 +  2.890 +
          1.837 +  1.690 +
          1.837 +  1.690 +
          2.446 +  2.250 +
          0.098 +  0.090 +
          3.924 +  3.610 = 46.831
DF = 11, P-Value = 0.000
```

Between 20:00-2:00

Chi-Square Test: OBS, UNOBS

Expected counts are printed below observed counts

	OBS	UNOBS	Total
1	8	4	12
	8.43	3.57	
2	8	4	12
	8.43	3.57	
3	7	5	12
	8.43	3.57	
4	8	4	12
	8.43	3.57	
5	10	2	12
	8.43	3.57	
6	9	3	12
	8.43	3.57	
7	9	3	12
	8.43	3.57	
Total	59	25	84

```
Chi-Sq =  0.022 +  0.051 +
          0.022 +  0.051 +
          0.242 +  0.571 +
          0.022 +  0.051 +
          0.293 +  0.691 +
          0.039 +  0.091 +
          0.039 +  0.091 = 2.278
DF = 6, P-Value = 0.892
7 cells with expected counts less than 5.0
```

An activity budget for Erethizon dorsatum (from behavioural observations between 20:00 and 2:00)

1 A review of the recording methods used to collect focal data

Source: Table 6, Figure 4

Chi-Square Test: Telemetry, Visual, Audible

Expected counts are printed below observed counts

	Telemetr	Visual	Audible	Total
1	13	179	81	273
	12.78	80.33	179.90	
2	22	78	156	256
	11.98	75.32	168.70	
3	1	95	274	370
	17.31	108.87	243.82	
4	2	2	105	109
	5.10	32.07	71.83	
5	13	63	162	238
	11.14	70.03	156.84	
6	10	7	61	78
	3.65	22.95	51.40	
7	12	35	189	236
	11.04	69.44	155.52	
Total	73	459	1028	1560

Chi-Sq = 0.004 +121.217 + 54.370 +
8.382 + 0.095 + 0.956 +
15.372 + 1.766 + 3.736 +
1.885 + 28.196 + 15.319 +
0.312 + 0.705 + 0.170 +
11.047 + 11.085 + 1.793 +
0.083 + 17.080 + 7.208 = 300.781

DF = 12, P-Value = 0.000
1 cells with expected counts less than 5.0

The general distribution of behaviour

Source: Table 7, Figure 5

Differences between hours 20:00 - 2:00

Kruskal-Wallis Test: inactive versus hour

47 cases were used
2 cases contained missing values
Kruskal-Wallis Test on inactive

hour	N	Median	Ave Rank	Z
0	7	1.000	27.5	0.73
1	7	1.000	20.6	-0.72
2	7	1.000	24.3	0.06
20	6	1.000	23.8	-0.05
21	7	1.000	24.3	0.06
22	6	1.000	19.4	-0.88
23	7	1.000	27.5	0.73
Overall	47		24.0	

H = 2.03 DF = 6 P = 0.917
H = 5.30 DF = 6 P = 0.505 (adjusted for ties)

Kruskal-Wallis Test: feeding versus hour

47 cases were used
2 cases contained missing values
Kruskal-Wallis Test on feeding

hour	N	Median	Ave Rank	Z
0	7	1.0000	28.4	0.91
1	7	0.5000	23.9	-0.03
2	7	0.5000	14.9	-1.91
20	6	1.0000	26.0	0.38
21	7	0.5000	21.1	-0.60
22	6	0.7500	24.9	0.18
23	7	1.0000	29.3	1.11
Overall	47		24.0	

H = 5.32 DF = 6 P = 0.504
H = 6.25 DF = 6 P = 0.396 (adjusted for ties)

Kruskal-Wallis Test: moving versus hour

47 cases were used
2 cases contained missing values
Kruskal-Wallis Test on moving

hour	N	Median	Ave Rank	Z
0	7	1.0000	24.4	0.07
1	7	1.0000	24.9	0.19
2	7	1.0000	24.4	0.07
20	6	1.0000	20.2	-0.73
21	7	1.0000	28.0	0.84
22	6	0.7500	16.6	-1.42
23	7	1.0000	28.0	0.84
Overall	47		24.0	

H = 3.46 DF = 6 P = 0.750
H = 8.09 DF = 6 P = 0.232 (adjusted for ties)

Kruskal-Wallis Test: travelling versus hour

47 cases were used
2 cases contained missing values
Kruskal-Wallis Test on travelling

hour	N	Median	Ave Rank	Z
0	7	0.00E+00	17.6	-1.34
1	7	5.00E-01	24.9	0.18
2	7	5.00E-01	29.4	1.12
20	6	2.50E-01	23.8	-0.05
21	7	5.00E-01	26.6	0.54
22	6	2.50E-01	23.8	-0.05
23	7	0.00E+00	22.1	-0.40
Overall	47		24.0	

H = 3.02 DF = 6 P = 0.806
H = 3.60 DF = 6 P = 0.730 (adjusted for ties)

Kruskal-Wallis Test: vocalising versus hour

47 cases were used
2 cases contained missing values
Kruskal-Wallis Test on vocalising

hour	N	Median	Ave Rank	Z
0	7	5.00E-01	22.7	-0.27
1	7	0.00E+00	20.4	-0.76
2	7	5.00E-01	22.7	-0.27
20	6	5.00E-01	25.0	0.19
21	7	5.00E-01	27.4	0.72
22	6	5.00E-01	27.8	0.72
23	7	5.00E-01	22.7	-0.27
Overall	47		24.0	

H = 1.60 DF = 6 P = 0.953
H = 1.80 DF = 6 P = 0.937 (adjusted for ties)

Differences within hours 20:00 -2:00

Kruskal-Wallis Test: 20 versus Behaviour

30 cases were used
5 cases contained missing values
Kruskal-Wallis Test on 20

Behaviou	N	Median	Ave Rank	Z
Feed	6	1.0000	16.5	0.31
Inactive	6	1.0000	20.7	1.61
Move	6	1.0000	17.7	0.67
Travel	7	0.5000	10.1	-1.86
Vocal	5	0.5000	13.1	-0.67
Overall	30		15.5	

H = 5.54 DF = 4 P = 0.236
H = 6.74 DF = 4 P = 0.150 (adjusted for ties)

Kruskal-Wallis Test: 21 versus Behaviour

Kruskal-Wallis Test on 21

Behaviou	N	Median	Ave Rank	Z
Feed	7	0.5000	14.1	-1.11
Inactive	7	1.0000	23.9	1.69
Move	7	1.0000	26.0	2.31
Travel	8	0.5000	11.8	-1.96
Vocal	6	0.5000	14.7	-0.88
Overall	35		18.0	

H = 11.16 DF = 4 P = 0.025
H = 13.83 DF = 4 P = 0.008 (adjusted for ties)

Kruskal-Wallis Test: 22 versus Behaviour

30 cases were used
5 cases contained missing values
Kruskal-Wallis Test on 22

Behaviou	N	Median	Ave Rank	Z
Feed	6	0.7500	16.8	0.41
Inactive	6	1.0000	18.8	1.01
Move	6	0.7500	16.8	0.41
Travel	7	0.5000	10.5	-1.72
Vocal	5	0.5000	15.4	-0.03
Overall	30		15.5	

H = 3.35 DF = 4 P = 0.501
H = 3.85 DF = 4 P = 0.426 (adjusted for ties)

Kruskal-Wallis Test: 23 versus Behaviour

Kruskal-Wallis Test on 23

Behaviou	N	Median	Ave Rank	Z
Feed	7	1.00E+00	19.7	0.49
Inactive	7	1.00E+00	24.5	1.88
Move	7	1.00E+00	24.5	1.88
Travel	8	0.00E+00	8.6	-2.95
Vocal	6	5.00E-01	13.3	-1.23
Overall	35		18.0	

H = 13.77 DF = 4 P = 0.008
H = 18.67 DF = 4 P = 0.001 (adjusted for ties)

Kruskal-Wallis Test: 0 versus Behaviour

Kruskal-Wallis Test on 0

Behaviou	N	Median	Ave Rank	Z
Feed	7	1.00E+00	20.4	0.70
Inactive	7	1.00E+00	26.0	2.31
Move	7	1.00E+00	23.0	1.44
Travel	8	0.00E+00	7.0	-3.46
Vocal	6	5.00E-01	14.7	-0.88
Overall	35		18.0	

H = 16.18 DF = 4 P = 0.003
H = 19.84 DF = 4 P = 0.001 (adjusted for ties)

Kruskal-Wallis Test: 1 versus Behaviour

Kruskal-Wallis Test on 1

Behaviou	N	Median	Ave Rank	Z
Feed	7	0.5000	18.3	0.08
Inactive	7	1.0000	22.0	1.15
Move	7	1.0000	25.1	2.06
Travel	8	0.2500	11.1	-2.16
Vocal	6	0.2500	13.8	-1.09
Overall	35		18.0	

H = 9.07 DF = 4 P = 0.059
H = 10.64 DF = 4 P = 0.031 (adjusted for ties)

Kruskal-Wallis Test: 2 versus Behaviour

Kruskal-Wallis Test on 2

Behaviou	N	Median	Ave Rank	Z
Feed	7	0.5000	12.0	-1.73
Inactive	7	1.0000	25.1	2.06
Move	7	1.0000	23.9	1.69
Travel	8	0.5000	13.9	-1.30
Vocal	6	0.5000	15.3	-0.70
Overall	35		18.0	

H = 9.79 DF = 4 P = 0.044
H = 11.49 DF = 4 P = 0.022 (adjusted for ties)

An overview: observed versus unobserved behaviour

Source: Table 8, Figure 6

Mann-Whitney Test and CI: Observed, Unobserved

Observed N = 7 Median = 69.17
Unobserv N = 7 Median = 30.83
Point estimate for ETA1-ETA2 is 43.33
95.9 Percent CI for ETA1-ETA2 is (26.67,55.01)
W = 77.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0022
The test is significant at 0.0021 (adjusted for ties)

Kruskal-Wallis Test: Observed versus hour

Kruskal-Wallis Test on Observed

hour	N	Median	Ave Rank	Z
0	7	85.83	28.1	0.63
1	7	85.83	27.5	0.50
2	7	60.00	19.3	-1.14
20	7	69.17	23.1	-0.39
21	7	74.17	27.9	0.57
22	7	57.50	20.0	-1.00
23	7	65.00	29.1	0.83
Overall	49		25.0	

H = 3.53 DF = 6 P = 0.741
H = 3.53 DF = 6 P = 0.740 (adjusted for ties)

The extent and distribution of behaviour as a proportion of observed time

Source: Table 9, Figure 7

Kruskal-Wallis Test: % Mins versus Behaviour

Kruskal-Wallis Test on % Mins

% Mins	N	Median	Ave Rank	Z
FEED	7	23.391	22.0	1.15
INACTIVE	7	57.409	31.6	3.92
MOVE	7	16.323	19.8	0.52
TRAVEL	7	3.688	8.2	-2.82
VOCAL	7	2.529	8.4	-2.76
Overall	35		18.0	

H = 26.05 DF = 4 P = 0.000
H = 26.06 DF = 4 P = 0.000 (adjusted for ties)

Source: Table 10, Figure 8

Between hours 20:00-2:00

Kruskal-Wallis Test: INACTIVE versus TIME

48 cases were used
1 cases contained missing values

Kruskal-Wallis Test on INACTIVE

TIME	N	Median	Ave Rank	Z
0	7	65.46	28.6	0.83
1	7	42.93	22.9	-0.32
2	7	51.94	23.0	-0.31
20	7	70.00	29.4	1.01
21	7	46.67	26.7	0.45
22	6	35.21	19.1	-1.01
23	7	56.14	21.0	-0.72
Overall	48		24.5	

H = 3.14 DF = 6 P = 0.791
H = 3.14 DF = 6 P = 0.791 (adjusted for ties)

Kruskal-Wallis Test: FEED versus TIME

48 cases were used
1 cases contained missing values

Kruskal-Wallis Test on FEED

TIME	N	Median	Ave Rank	Z
0	7	12.908	26.6	0.42
1	7	10.345	22.9	-0.32
2	7	2.830	19.9	-0.93
20	7	18.333	23.2	-0.26
21	7	5.882	23.4	-0.23
22	6	24.208	27.1	0.48
23	7	24.592	28.8	0.88
Overall	48		24.5	

H = 1.95 DF = 6 P = 0.924
H = 1.97 DF = 6 P = 0.922 (adjusted for ties)

Kruskal-Wallis Test: MOVE versus TIME

48 cases were used
1 cases contained missing values
Kruskal-Wallis Test on MOVE

TIME	N	Median	Ave Rank	Z
0	7	8.494	21.9	-0.54
1	7	13.559	26.3	0.37
2	7	14.855	27.4	0.60
20	7	13.166	20.7	-0.77
21	7	16.981	26.1	0.34
22	6	9.079	16.5	-1.50
23	7	17.488	31.4	1.42
Overall	48		24.5	

H = 4.95 DF = 6 P = 0.550
H = 4.96 DF = 6 P = 0.549 (adjusted for ties)

Kruskal-Wallis Test: travel versus TIME

48 cases were used
1 cases contained missing values
Kruskal-Wallis Test on TRAVEL

TIME	N	Median	Ave Rank	Z
0	7	0.00E+00	18.4	-1.26
1	7	1.19E+00	26.9	0.50
2	7	4.26E+00	28.6	0.83
20	7	0.00E+00	22.4	-0.42
21	7	3.45E+00	27.1	0.53
22	6	4.31E-01	26.3	0.33
23	7	0.00E+00	22.1	-0.48
Overall	48		24.5	

H = 2.83 DF = 6 P = 0.830
H = 3.24 DF = 6 P = 0.779 (adjusted for ties)

Kruskal-Wallis Test: vocal versus TIME

48 cases were used
1 cases contained missing values
Kruskal-Wallis Test on vocal

TIME	N	Median	Ave Rank	Z
0	7	8.47E-01	20.1	-0.89
1	7	0.00E+00	20.9	-0.73
2	7	1.47E+00	27.7	0.66
20	7	8.33E-01	23.9	-0.13
21	7	1.89E+00	26.3	0.37
22	6	5.01E+00	31.8	1.36
23	7	8.33E-01	21.9	-0.54
Overall	48		24.5	

H = 3.49 DF = 6 P = 0.745
H = 3.68 DF = 6 P = 0.719 (adjusted for ties)

Within hours 20:00-2:00

Kruskal-Wallis Test: 20 versus BEHAVIOUR

Kruskal-Wallis Test on 20

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	1.83E+01	18.5	0.14
INACTIVE	7	7.00E+01	30.0	3.46
MOVE	7	1.32E+01	18.6	0.16
travel	7	0.00E+00	10.7	-2.10
vocal	7	8.33E-01	12.2	-1.67
Overall	35		18.0	

H = 15.41 DF = 4 P = 0.004
H = 16.05 DF = 4 P = 0.003 (adjusted for ties)

Kruskal-Wallis Test: 21 versus BEHAVIOUR

Kruskal-Wallis Test on 21

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	5.882	17.1	-0.25
INACTIVE	7	46.667	30.9	3.71
MOVE	7	16.981	20.7	0.78
travel	7	3.448	11.6	-1.86
vocal	7	1.887	9.7	-2.39
Overall	35		18.0	

H = 18.89 DF = 4 P = 0.001
H = 18.95 DF = 4 P = 0.001 (adjusted for ties)

Kruskal-Wallis Test: 22 versus BEHAVIOUR

30 cases were used
5 cases contained missing values
Kruskal-Wallis Test on 22

BEHAVUIO	N	Median	Ave Rank	Z
feed	6	24.2075	19.2	1.14
INACTIVE	6	35.2120	19.1	1.11
MOVE	6	9.0790	15.0	-0.16
travel	6	0.4310	12.0	-1.09
vocal	6	5.0090	12.3	-1.01
Overall	30		15.5	

H = 3.82 DF = 4 P = 0.431
H = 3.87 DF = 4 P = 0.424 (adjusted for ties)

Kruskal-Wallis Test: 23 versus BEHAVIOUR

Kruskal-Wallis Test on 23

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	2.46E+01	22.4	1.26
INACTIVE	7	5.61E+01	28.3	2.97
MOVE	7	1.75E+01	21.6	1.03
travel	7	0.00E+00	9.1	-2.56
vocal	7	8.33E-01	8.6	-2.70
Overall	35		18.0	

H = 20.24 DF = 4 P = 0.000
H = 20.48 DF = 4 P = 0.000 (adjusted for ties)

Kruskal-Wallis Test: 0 versus BEHAVIOUR

Kruskal-Wallis Test on 0

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	1.29E+01	23.0	1.44
INACTIVE	7	6.55E+01	30.4	3.59
MOVE	7	8.49E+00	18.6	0.16
travel	7	0.00E+00	8.2	-2.82
vocal	7	8.47E-01	9.8	-2.37
Overall	35		18.0	

H = 22.87 DF = 4 P = 0.000
H = 23.26 DF = 4 P = 0.000 (adjusted for ties)

Kruskal-Wallis Test: 1 versus BEHAVIOUR

Kruskal-Wallis Test on 1

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	1.03E+01	18.8	0.23
INACTIVE	7	4.29E+01	27.0	2.60
MOVE	7	1.36E+01	21.7	1.07
travel	7	1.19E+00	13.0	-1.44
vocal	7	0.00E+00	9.5	-2.45

Overall	35		18.0

H = 12.84 DF = 4 P = 0.012
H = 13.07 DF = 4 P = 0.011 (adjusted for ties)

Kruskal-Wallis Test: 2 versus BEHAVIOUR

Kruskal-Wallis Test on 2

BEHAVUIO	N	Median	Ave Rank	Z
feed	7	2.830	15.3	-0.78
INACTIVE	7	51.936	28.7	3.09
MOVE	7	14.855	18.6	0.16
travel	7	4.255	13.1	-1.42
vocal	7	1.471	14.4	-1.05
Overall	35		18.0	

H = 10.67 DF = 4 P = 0.031
H = 10.85 DF = 4 P = 0.028 (adjusted for ties)

Foraging behaviour

Tree use by porcupines

Source: Table 12

Chi-Square Test: conifer, deciduous

Expected counts are printed below observed counts

	conifer	deciduou	Total
1	10	9	19
	12.67	6.33	
2	12	2	14
	9.33	4.67	
Total	22	11	33

Chi-Sq = 0.561 + 1.123 +
0.762 + 1.524 = 3.970
DF = 1, P-Value = 0.046
1 cells with expected counts less than 5.0

Tree descents by porcupines

Source: Table 13, Figure 10

Chi-Square Test: hour and number of recorded descents

Hour	21:00	22:00	23:00	00:00	01:00	02:00	03:00	04:00
Observed	5	1	2	1	2	6	4	2
Expected	2.875	2.875	2.875	2.875	2.875	2.875	2.875	2.875

Chi-sq=8.65, DF=7, CV=14.07

A composition by HRJ:

Les Porcs-Epics du Parc du Bic

or

Summer 2002

At dusk, a lumbering sense of urgency
awakens those who 'ought -
descend their daytime hideaways
to start the business of the dark.
And yet, they yawn, and tally still.

And in what splendid castles they abide:
the sun-soaked cedar atop a cliff
with view o'er sea sublime,
Or else a shady meadow niche
for the more conservative inclined.

But of all the daylight residences
on offer Parc-Bic-wide,
a generous, cozy, sheltered tree
upon the beach must fetch a fee
and be the most exclusive prize.

Lovers at Epinette, been and gone,
pink to purple cloak unravels,
and stars descend with pressing issue.
Awake! Revive! Get going! *Move!*
The night is young, but dawn 'waits none.

The thickening dark is not all friendly
(perils wander in the parc)
- those with nets and needles plenty.
A porcupine had best avoid them
and yet sleep a little more.

Eventually: calm resignation
to the nights deliberate ventures;
A shake, a sneeze, a scratch, a shuffle -
earnest gestures to depart.
A quick descent, and off to work.

Into Action, (no more lazy) -
fast departure, bustling, bear-like,
bulldozing through unyielding shrub.
To rain-soaked meadows and beyond -
hunger drives like madness pending.

And yet, to watch 'em feed and doze,
it seems no urgent matter.
Why rush, when safe in tree-top diner?
Why not delay, digest and ponder?
(on last nights business or all else?)

Perhaps rehearsing safety-schemes,
to ruse the capture crew.
Or else eating with great care and skill
(Chew your food! No mess! No noise...)
all to defy a listening ear.

It's with surprise that night meets day -
cool, tranquil shroud becoming gold,
heralded in by joyful birds.
At last! Relief from darkened cloud.
Bejewelled night turns pink, behold!

And so with dawn, another day!
Thus porcupines, w'haphazard track,
will find another place to nap.
The nights endeavours all but done
it's time to quietly wind-down now.

And I had best not write some-more -
in case someone finds out
my faithful fieldbook has been used
to write this poem
(clear abuse!).

Activity budget & foraging behaviour of the North American porcupine

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Introduction

Erethizon dorsatum is a medium sized, semi-arboreal folivorous rodent. Living predominantly on tree foliage is not straightforward: there may be lower mass limits on digestive efficiency[1] (as digestive efficiency ∝ gut size ∝ body mass[2,3,4]) yet upper mass limits on foraging capability[2]. How does the North American porcupine maintain its lifestyle in the trees with such success?

AIMS: What methodology should be used to study the natural behaviour of porcupines? Can these methods be used to devise an activity budget and explore foraging behaviour?

Field Site & Methods

Field site

Located in 33.2 km^2 Parc du Bic National Park, south west Quebec, Canada

- 2 km^2 study area of mixed forest habitat with adjacent arable farmland, salt-marsh and rocky shore habitat
- Seven individually tagged adult female porcupines were radio-collared
- Field work carried out 8 May - 3 July 2002

Methods

- Continuous observations on animals 20h - 2h
- Categories of behaviour recorded: ***Feeding, Vocalising, Travelling, Moving, Inactivity****
  Inactivity: calculated from total observation time - (minutes of recorded behaviour)
- Data was collected using a combination of 'visual' (infra-red night vision equipment), 'audible' & 'radio-telemetry' to record behaviour

So....What do porcupines do in the dark??

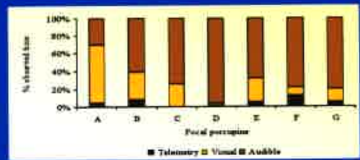
Where were porcupines seen?

During the night most porcupine behaviour was recorded whilst the animals were in arboreal locations ([illegible] % of observation time porcupines were observed in trees, [illegible] % of the time they were seen on the ground)

Activity budget

How was data recorded?

Analysis of methods

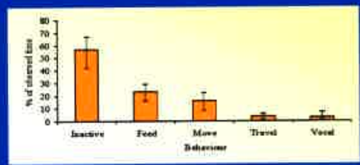


68% of behaviour was collected using audible methods, 28 % by visual observations & 5 % by telemetry

The difference between animals in the recording methods used to record their behaviour was significant ([illegible] P<0.001)

How did porcupines divide their time?

Activity budget

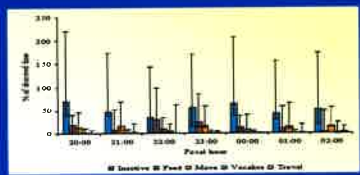


57 % of observed time porcupines were inactive, 23 % feeding, 16 % moving & & 3 % vocalising

There was a significant difference between time spent engaged in different behaviours (Kruskal Wallis P<0.001)

How was time divided across hours?

Activity budget across the night



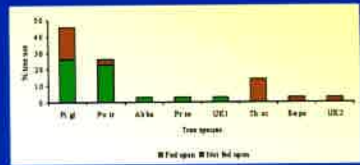
Across hours there were no significant differences in the extent porcupines were engaged in different behaviours (Kruskal Wallis P>0.05)

Within all hours excluding 22h there were significant differences in how porcupines spent their time (Kruskal Wallis 20h P=0.003 21h P=0.001 23h=P<0.001 0h P<0.001 1 h P=0.011 2h P=0.028 22h P=0.424)

Foraging behaviour

Were trees used for feeding or resting?

Tree use



Porcupines used white spruce (*Pi gl*) 46% of the time, trembling aspen (*Po tr*) 26 % & white cedar (*Th oc*) 15 %. White birch (*Be pa*), balsam fir (*Ab ba*), wild cherry (*Pr se*) and two unidentified species were also used

Trees could be used for feeding purposes or for non-feeding behaviour such as resting

There was a significant difference between tree use and broad category of tree type (deciduous vs conifer) ([illegible] P=0.05)

Deciduous trees seemed to be favoured for feeding use although both deciduous and coniferous trees were browsed upon almost equally

Conclusions

Most porcupine behaviour was recorded whilst animals were in tree locations, predominantly by just listening to sounds of activity or movements.

Porcupines were mostly inactive. Porcupines are hind-gut fermentors with an enlarged, specialised gut to retain digesta particles and a rich assortment of microfauna which assist in the breakdown of indigestible fibre[5]. There may be physical restrictions on the volume of food the gut can process, impeding activity whilst fermentation and digestion takes place.

Feeding is an important activity for folivores as the nutritional density of leaf plant material is relatively low although leaves are spatially and temporally abundant.

Dietary range was limited. Porcupines may be able to specialise on certain trees due to adaptations enabling them to detoxify potentially harmful anti-herbivore compounds, often specific to particular trees[6]. Dietary specialisation may allow porcupines to exploit food resources considered unpalatable to herbivorous competitors.

References

[illegible]

The Population Dynamics of Red and Grey Squirrels in Britain

0110527j

*Boyd Watt, 1923**

'The grey squirrel can never become wide-spread and dominant like our other introduced animals, the rabbit and the brown rat....
If a comparison has to be made...make it with the fallow-deer, a park and woodland animal, an attractive and valuable addition to our fauna.'

The grey squirrel *Sciurus carolinensis* has been present and apparently thriving in Britain since being released and further translocated at various locations around the turn of the century. Individuals were introduced from its native Eastern USA into England and Wales from 1876 to 1929, into Scotland from Canada between 1892 and 1920 and into Ireland from England in 1911. (Teangana et al., 2000a & b).

Simultaneously, the indigenous red squirrel *Scuirus vulgaris* has disappeared from grey colonised sites. (Reynolds, 1985). Evidence of changes in the two species' distributions comes from nine large-scale national surveys since the 1930s. Initial surveys centred on the notable success of the grey 'novelty' species in recognition that the grey was a potential hardwood timber pest species and therefore of economic importance. (Lloyd, 1983). In recent years there has been increasing biological interest in the declining fortunes of the endemic red squirrel. From the 1930 survey onwards the grey has rapidly expanded its range. In 1945 the red squirrel was more widely distributed than the grey but by 1971 the grey occupied almost four times more area of England and Wales than the red (Lloyd, 1983). The grey squirrel is now ubiquitous in almost all of central and southern England, Wales, some lowland areas of Scotland, Eastern and Central Eire and Northern Ireland (Lloyd, 1983; Reynolds, 1985; Gurnell & Pepper, 1993; Teangana *et al.*, 2000a; Teangana *et al.*, 2000b). (The current range expansion rate of the grey in Ireland is estimated at 13.4 km/year (Teangana *et al.*, 2000a).) The red is presently on the verge of extinction in Wales and England, with mainland Central and Southern England fostering squirrels in only four areas isolated within grey-dominated counties: East Anglia, Staffordshire, Derbyshire and Merseyside. (Gurnell & Pepper, 1993). Scotland remains a red squirrel stronghold and

* From: Williamson M (1996). The Process of Spread, Spread With Ecological Interaction in: Biological Invasions. (ed. By MB Usher, DL De Angelis & BFJ Manly), pp. 107-114, Chapman & Hall. London.

grey squirrel advancement is slow (Forestry Commission records, 1980-1994; Bryce, 1997).

General patterns of species distribution from the survey data span over fifty years. In recent decades there has been a surge of interest in the fundamental ecological processes that may be influencing the squirrels' changing fortunes. Three hypotheses might explain the dynamics of the species: I) environmental change, affecting red populations irrespective of the greys, II) competition with the invading grey, III) disease, perhaps involving the grey (Reynolds, 1985; Okubu *et al.*, 1989). This review includes these main avenues of interest in an attempt to elucidate some of the main issues pertaining to red and grey squirrel demography in the current period.

There have been perturbations in the UK red squirrel population that are undoubtedly unrelated to the presence of the grey. The red squirrel population in Scotland crashed almost to extinction in the 17th and 18th centuries before grey squirrels were first released. In the late 19th and early 20th century the species became exceedingly abundant, stimulating culls to reduce conifer plantation damage (Highland Squirrel Club, 1903-1946). A widespread decline followed in the 1920s and since this period, as the greys became increasingly common there were local fluctuations in red squirrel distribution. (Lloyd, 1983). From this it may be inferred that there are demographic processes intrinsic to red squirrels and their specific use of a changing UK forest habitat that may explain some of the observed current distribution.

It is worthy of note to mention that in North America the native American red squirrel (*Tamiasciurus hudsonicus*) occupies a niche separate to the Eastern grey squirrel and that these niches seldom overlap. (Okubu *et al.*, 1989). There, American red squirrel distribution is closely associated with (coniferous) pine and spruce-dominated forests (Gurnell, 1987) whilst the grey squirrel exists in mixed hardwood forest. (Okubu et al, 1989). Although the British red squirrel has adapted to live in both types of forest their current distribution in the UK, in the presence of grey squirrels, appears associated with the remaining conifer dominated forest refuges.

There exist both similarities and differences between the species. Principally there are marked differences in pelage, body size and three-dimensional use of habitat. The red squirrel is a 'low-density' very arboreal creature, agile and lightweight (body mass *ca.* 300g, Bryce *et al.*, 2001), well adapted for moving fast on the slim elevated branches of

coniferous and deciduous trees. The much larger and stockier grey squirrel is a 'high-density' animal (body mass *ca.* 570g, Bryce *et al.*, 2001), suited to living in hardwood forests and with more terrestrial habits (Gurnell, 1987). Differences in three-dimensional use of habitat have been identified. Red squirrels spend proportionally more time per year in the forest canopy than greys (67% of their active time in deciduous forest canopy compared to just 14% by greys; Racey 1986).

Both red and grey squirrels show seasonal weight changes, accumulating extra weight in December/January. The weight change for red squirrels has been recorded as 11.9% compared to 22.6% in greys. The smaller reserves may disadvantage the red squirrel during winter seasons of poor energy yield. (Racey, 1986).

The two species may occupy the same forest habitat. Modern temperate forests of North America and Europe are remarkably similar in tree species composition. The natural climax community is usually formed of a mixture of deciduous broad-leaves such as oak, beech and maple in association with hardwood varieties such as lime, elm, ash, walnut and chestnuts. (Gurnell, 1987). Similarities between Eastern US forest habitat and the forest mosaic of the UK was likely to be to the alien grey squirrel's advantage when animals were first introduced. The habitat within the UK has changed over the last millennia with oak-dominated deciduous woodland replacing mixed broadleaf/conifer and coniferous forest. Before 1920 oak/hazel woodlands were 40% of the timber planted in Britain. (Kenward & Holm, 1993). Subsequent changes in woodland management practices included hazel clearance. This may have contributed directly to the general decline of red squirrels in the 1920s as red squirrel demography has been positively correlated with hazel crop abundance (Wauters *et al.*, 2001). Low population densities of red squirrels during the grey's expansion in the 1930s may have reduced the ability of the reds to re-colonise previously occupied habitat. Additionally, grey squirrels have adapted remarkably well to the urban environment that has inevitably replaced large forest areas (Bowers & Breland, 1996).

Large tracts of continuous forest no longer exist in much of the UK. Coupled with the loss of valuable hedgerow corridors between woodlands (Wauters, Casale & Dhondt, 1994), this will have reduced the dispersal ability of individuals, resulting in genetic isolation between woodlands. This has implications for both species, as it will increase the potential for local population extinction. One might assume that the grey squirrel population suffers from a founder effect of limited genetic diversity. However, the grey squirrel population in

Britain does not originate from a single introduction but stems from numerous introductions at different times from various genetic sources. Consequently the grey squirrel currently shows greater genetic diversity than the red squirrel (Wauters, Casale & Dhondt, 1994; Gorman, 1998).

The availability of preferred food sources differs between forest types and this may strongly influence squirrel distribution. Density and productivity of both species has been correlated with tree seed crops for both species in deciduous and conifer woodland (Kenward *et al.*, 1998). Diet is similar when the two species are allopatric (Bryce *et al.*, 2001). The primary food item is tree seeds and both species use secondary food items such as flowers, buds, fungi and insect larvae when principal food items are scare (Gurnell, 1987). Grey squirrels specialise on the large-seeds of broad-leaved trees, whilst red squirrels use small-seeds preferentially (Bryce *et al.*, 2001). Conifer plantations offer a high availability of small pine seeds which are fed upon by red squirrels intensively in summer, autumn (Wauters *et al.*, 2001) and winter (Wauters & Casale, 1996). The cones are clipped from branches in the canopy (Wauters & Dhondt, 1992) for which activity the squirrels are well adapted. The main crop of oak woodland is acorns, which ripen late September-late November. The availability of acorns contributes to the success of grey squirrels (Gurnell, 1996). Kenward & Holm (1993) demonstrated that the red squirrel has a poor tolerance of the tannins found in acorns, whilst grey squirrels may thrive on them. Red squirrels rarely consume acorns to the same extent (Wauters *et al.*, 2000).

Cone crop production varies widely with 4-fold difference between sites and 50-fold variation between years in spruce species (Lurz *et al.*, 1997). Such excess of seeds in random years is known as a 'mast year' crop. Seasonal variation may influence red squirrels tremendously as the products of a conifer mast year influences reproductive potential in mature females (Wauters and Dhondt, 1995). Indeed tree seed crops of both deciduous and conifer forests correlated positively with pre-breeding densities and subsequent productivity of both squirrel species (Kenward *et al.*, 1998; Wauters *et al.*, 2000).

Habitat differences also affect space use by squirrels. Both species do not defend resource-limited territories but occupy home ranges with intensively used core areas. In red squirrels, home range size varies with sex and season (Wauters & Dhondt, 1992). The use of space in different habitats has been allied with food availability in different forest types. In stable habitats where food type is predictable (as in coniferous woodland) red squirrels

show high home range fidelity and densities are high. In more heterogeneous habitats with widely spaced resources, such as deciduous habitat, red squirrels may establish larger home ranges and exist at lower densities (Lurz *et al,* 1997). Discontinuous fragmented woodland may also represent such a habitat and these areas also support lower red squirrel densities than continuous coniferous and deciduous forest (Wauters, Casale & Dhont, 1994). In addition, the woodland composition may influence different degrees of territoriality in individuals. In deciduous habitat, red squirrels have a higher tolerance of encounters with individuals of both species (Wauters & Gurnell, 1999), and there may be a greater extent of overlap of core home range areas (Wauters & Dhondt, 1992), potentially increasing resource competition.

Recruitment may be affected by adjacent habitat type, as the proximity of conspecifics may be necessary to support existing densities. Grey squirrels in conifer woodlands suffer higher mortality (perhaps due to ground-level predators) and rely on immigration to maintain densities (Wauters *et al.*, 2000). Grey squirrels may thus be at a disadvantage in conifer-only sites due to isolation, whilst reds may suffer from the close proximity of grey colonised deciduous habitat due to increased pressure on resources. It has been suggested that the rate of juvenile recruitment is a key factor affecting grey squirrel success, and this is lower in conifer forest areas where both species are present than in grey only sites (Wauters *et al.*, 2000).

Both species store food by 'scatterhoarding' whereby one or more food items are placed within each hoarding site on the ground, with hundreds or thousands of these distributed within a home range area (Wauters & Casale, 1996). Cached food represents an important resource. It allows for a conserved energy supply to be exploited when the food availability is less predictable or the niche width narrower (in early spring months). The potential energy available through scatterhoarded food items is predicted to be greater in deciduous versus conifer woodland (Wauters & Casale, 1996). Of course, profit from this food storage method is related to the extent of competition between hoarders, and ideally all squirrels are retrieving as much as they hoard. Red squirrels may not be profiting from their scatterhoarded reserves as grey squirrels are. Indeed, resource competition may occur between reds and greys as the reds retrieve only 50 % of acorns they hoard (Wauters & Casale, 1996), a key food item for grey squirrels. In addition, as grey squirrels spend more active time on the ground than reds (Racey, 1986), they may have a higher probability of encountering cached resources. Thus, it appears due to feeding behaviour differences

between reds and greys, the native red may be scatterhoarding inefficiently in woodland areas supporting both species, resulting in a negative energy imbalance for itself.

An additional and important intrinsic demographic detail may be the conservative reproductive potential of the red squirrel compared to the grey as fecundity and fitness of the squirrels also differs. Red squirrel females have a spring litter size of 2-3 in contrast to greys producing 4-5 (Okubo, 1989). Under optimum conditions of adequate food and continued positive energy balance both species may produce a second litter in early summer. But the lower overall fecundity of red squirrels may have a considerable influence on population demography as females failing to secure a home range adequate to supply critical resources may not attain reproductive condition at all (Wauters & Dhondt, 1995). Indeed, evolution without the presence of a grey competitor and the continuous, more homogeneous habitat of the past may have favoured such a strategy, as resources and the capacity to disperse were not limited resulting in less pressure on reproductive ability. Reproductive output may be enhanced in greys in mixed or pure deciduous habitat, and limited in red squirrels in areas where the species co-habit. Therefore, reproductive output may be influencing the red squirrel population rather than adult survival alone (Gurnell & Pepper, 1993).

It has been popularly assumed that interspecific competition occurs between the two species through direct aggressive encounters, and that the larger grey is dominant. This is a gross oversimplification. Although the two species may encounter one another within the same habitats, overtly aggressive behaviour has yet to be recorded. (Kenward & Holm, 1993; Wauters & Gurnell, 1999). The presence of grey squirrels does not affect the daily activity patterns of red squirrels (Wauters & Gurnell, 1999; Wauters *et al.*, 2000). As the two species use different vertical dimensions within the forest for much of the year with reds spending more time arboreally foraging (Racey, 1986), the two species might be considered able to partition the habitat successfully and avoid close contact. However, in what appears a competitive exclusion effect the largest fragmented populations of red squirrels are located in large conifer forests, seemingly 'retreating' from optimum grey habitat. Average densities for red and grey squirrels in conifer forests and red squirrels in broad-leaved forests are similar although densities of grey squirrels in broad-leaved forests are several times higher (Gurnell, 1991). Modelling attempts by Rushton *et al.*(1997) used GIS (Geographical Information System) landscape scale projections of real population estimates, incorporating parameters of grey interference, to predict that competitive exclusion by the grey squirrel is largely responsible for its' observed success.

When tested, this theoretical approach proved unsatisfactory (Wauters & Gurnell, 1999). The presence of grey squirrels did not provoke behavioural avoidance or interfere with breeding in red squirrels (Wauters & Gurnell, 1999).

A more plausible form of antagonistic behaviour is intraspecific aggression directed at non-kin and non-residents of the same species as in grey squirrels (Koprowski, 1993) or intraspecific and interspecific competition for shared resources in overlapping home ranges in patches of high squirrel density. If interspecific resource competition is a factor contributing to the grey squirrels' persistence it has the potential to cause serious imbalance. As demonstrated by Okubu (1989) in a continuous deterministic model, even low levels of direct red-grey competition may lead to red squirrel extinction.

The effect of competition between the species is likely to be subtle. Although in the presence of grey squirrels, red squirrels may select poorer quality habitat (Wauters *et al.*, 2000), the most likely explanation for the red displacement by greys is an efficiency by grey squirrels at exploiting resources, particularly food (Gurnell & Pepper, 1993). There may be considerable potential for dietary competition in deciduous woodland. It is apparent that grey squirrels are better able to utilise the fruits of deciduous woodland, where seed crops are acorn-biased and in general more variable, considering that oak acorns are correlated with grey fitness (Kenward *et al.*, 1998). Although red squirrels may move in to exploit conifer seed when cone crops are good, the grey squirrel is more adaptable and better able to retreat to deciduous patches when these resources fail. Red squirrels may remain in the conifer patches throughout the year when grey squirrels are present although this may affect their ultimate survival, as they become limited to this narrow niche (Gurnell & Pepper, 1993).

There is some evidence of outbreaks of disease affecting red squirrel populations. 1931 accounts (Middleton) describe an outbreak of 'distemper' amongst squirrels. Accounts registered in 1927 and 1960 describe red squirrels with purulent eyes similar to the 'myxomatosis' observed in rabbits (Reynolds, 1985). The disease mentioned is parapoxvirus, first detected in a diseased animal in 1981 and isolated in 1984. It has been suggested that outbreaks of the disease may influence local population decline in red squirrels (Reynolds, 1985; Gurnell & Pepper, 1993; Rushton *et al.*, 2000). There is evidence that grey squirrels are acting as a reservoir host for the virus as apparently healthy animals have been found to be exposed to the disease (Sainsbury *et al.*, 2000). Low severity of the infection in greys may enable the disease to spread rapidly in grey hosts. A

stochastic, individual based model (Rushton *et al.*, 2000) has predicted that parapoxvirus could have lead to red squirrel extinction in Norfolk due to the combined effects of a fast expansion rate of the disease carrying greys, and close encounter rates between the species in shared habitats. By consideration of the above, disease transmission may be considered competition because the virus does offer greys an advantage.

Changes in the forestry structure within the UK may have initially favoured the grey squirrel. An indirect consequence of this and other demographic factors are contributing to a reversal of squirrel species representation in the UK.

Fragmentation effects can affect individual dispersal considerably. Combined with UK-wide loss in favoured (conifer) habitat, the resulting isolated conifer refuges with their random seasonal seed production are unlikely to sustain red populations. An intrinsically low fecundity (compared to greys), lowered recruitment rates relating to isolation, and diminishing genetic diversity will not favour red expansion in grey-occupied woodland or areas where grey dominated habitat envelopes red-only areas. Red squirrel individual reproductive success may be affected if fitness is reduced due to a tolerance of greys in species-mixed areas, coupled with a reduced ability to utilise the resource potential of the habitat. Additionally, disease incidence will sometimes predispose red squirrels to replacement by greys. Future consideration of the effects of interspecific competitive exclusion versus resource competition may further clarify issues pertaining to red squirrel displacement.

The costly procedures of modifying the structure of woodland fragments to reverse the current pattern of squirrel distribution may not prove effective if demographic traits of red squirrels will not improve their survival and breeding success. If this is the case, intensive conservation efforts to maintain existing red squirrel strongholds, and a programme to increase its genetic diversity may conserve the red squirrel, albeit only in managed pockets.

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Review the underlying causes, and potential solutions, to the current conflict between agriculture and conservation in the management of goose populations in Scotland

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Introduction

Lowland grassland areas throughout Britain provide numerous annual winter refuge sites for over 400,000 migratory, wild geese of six species: pink-footed geese *Anser brachyrhynchus*, greylag geese *A. anser*, Greenlandic and Eurasian white-fronted geese *A. albifrons*, bean geese *A. fabalis*, barnacle geese *Branta leucopsis* and dark-bellied and light-bellied brent geese *B. bernicla* (Vickery & Gill, 1999). These seasonal visitors spend at least part of their winter in the UK foraging in flocks on land of agricultural importance (Gill *et al.,* 1996; Kirby *et al.,* 1999) close to nearby roosts. It has been proposed that their foraging presence may cause considerable agricultural disturbance and a detrimental economic impact on the land (Owen, 1990; Kirby *et al.,* 1999). Consequently, there has been a great deal of interest directed towards defining a cost-effective strategy for land-managers to avert the impact of increasing numbers of wild geese utilising land of agricultural importance, whilst recognising that some of these goose species have important conservation status. Scotland serves as an important over-wintering site for five of the six aforementioned species and currently supports the majority of UK wintering geese (Table 1, reproduced from Kirby *et al.,* 1999). This review provides an overview of some of the current issues pertaining to the management of goose populations in Scotland, with reference to UK-wide wild goose research.

Goose Populations in Scotland

Throughout the UK, Icelandic pink-footed and Icelandic greylag geese are the most numerous winter goose migrants, with the majority wintering in Scotland (Vickery & Gill, 1999; Patterson *et al.*, 1989). The main population of Greenlandic white-fronted geese and the Greenland population of barnacle geese winter on the inner hebridean island of Islay.

The Solway coast (SW Scotland) harbours the Svalbard barnacle geese winter population. The bean goose winters at the Carron and Avon Valleys in central Scotland (also in Norfolk). It should be realised that there are also geese present in Scotland year-round. A native population of ca. 9000 Scottish greylag geese are permanent residents of the Western Isles and northern Scotland (Vickery & Gill, 1999), and ca. 3000 naturalised greylag geese and ca. 1000 Canada geese also reside in Scotland.

Of the six aforementioned species, five are considered agricultural pests due to a recent substantial increase in their numbers wintering in the UK. Table 2, (reproduced from Vickery & Gill, 1999) describes significant changes in the British wintering goose population size between 1960 and 1995. Of the species wintering in Scotland, Table 2 illustrates a four-fold increase in the pink-footed geese, a three-fold increase in Icelandic greylag geese, a notable seven-fold increase in Greenland white-fronted geese, and a three-fold increase in barnacle geese.

Why have goose populations increased so substantially?

It has been proposed that the population size of wild geese wintering in the UK may have been previously limited by the distribution and quantity of winter forage (Owen & Black, 1991). Modern agricultural practises are creating an increasingly managed, open, and 'improved' agricultural landscape. Under these conditions goose populations may be benefiting from reduced levels of winter mortality due an increased availability of quality forage. In addition, an increasingly mild winter climate is likely to enhance individual survival.

Furthermore, greater levels of protection and more controlled attitudes towards hunting have unequivocally enhanced survival in geese. In the early 20th century there was growing concern relating to the degree of organised culling and egg harvesting undertaken by local communities at the birds Arctic breeding grounds (Wildfowl Inquiry Sub-Committee, 1941). Unease regarding the declining state of wildfowl populations wintering in the UK initiated changes in legislation, initially implementing shooting restrictions to avoid excessive kills in order to maintain suitable populations for harvesting. The 1954 Protection of Birds Act provided the first comprehensive protection of wild birds, their nests and eggs (Owen *et al.*, 1986). Presently, the amended Wildlife and Countryside Act 1981 provides the legal framework for the conservation and management of geese in Britain. Current hunting restrictions protect wild populations of geese of all species

throughout the UK, with species specific levels of protection related to the quarry status of the bird (Kirby *et al.*, 1999). In compliance with the 1971 Ramsar Convention and EU Birds Directive, wetland habitats encompassing suitable roost and forage areas have been developed and are managed to provide safe havens (Owen, 1990; Kirby *et al.*, 1999).

Protection status extends beyond the British Isles. Although resident in the UK for several months, the migration route of the geese to their summer nesting grounds, and the breeding grounds themselves encompass an international community. Therefore, the geese benefit from various levels of national and international species protection (Table 3, reproduced from Kirby *et al.*, 1999). Major changes in geese numbers have occurred since the 1980s, a period following the implementation of much international and local protection (Owen, 1990). There is strong evidence that the recent increase in population numbers of Russian-breeding barnacle geese, brent geese and white-fronted geese may be due to reduced shooting of the birds throughout their ranges (Ebbinge, 1991). Presently, under the Birds Directive and the Bonn Convention (on the Conservation of Migratory Species of Wild Animals), those wishing to obtain a licence for killing geese to protect livestock or crops must first provide evidence of serious damage, and that no satisfactory alternative solution exists. Recent Action Plans implemented in 1996 commit participating countries to actively seek to manage conflict surrounding bird and human interests (Kirby *et al.*, 1999).

Interestingly, it appears goose productivity and seasonal population growth are currently unlimited by intrinsic regulatory processes. There is little evidence to suggest that goose populations are suffering density-dependent effects at their remote northern breeding grounds as a result of enhanced populations. Barnacle geese represent the only species in which recent evidence of density dependent regulation has been observed (Owen, 1990; Larsen & Forslund, 1994; Loonen *et al.*, 1997).

What agricultural conflicts does the presence of the geese evoke?

Discontentment arises amongst landowners whose property attracts geese due to the combination of several factors: the large numbers of birds intensively foraging upon agricultural land, the birds late winter/spring grazing feeding habits, and flock year to year site-fidelity in utilising specific fields which affect particular farms disproportionately.

Most migratory goose populations arrive in Scotland in September/October, and leave in March/April (Kirby *et al.*, 1999). During this period, they feed by day almost exclusively

upon farmland, whilst roosting at night in large numbers at locations often less than 5km away (Patterson *et al.,* 1989; Owen, 1990). Geese are highly gregarious birds and typically forage in undisturbed open field locations. In the absence of disturbance large flocks of up to 1000+ birds may develop (Newton & Campbell, 1973; Summers, 1990).

In autumn, the impact of geese feeding on arable land is considered minimal. Grass in pastureland has ceased growing, and the remains of harvested autumn crops are frequently left to rot in the soil as wastage (Kear, 1990). Greylags and pink-footed geese consume stubble and waste root crops, white-fronted and barnacle geese graze on the senescing grass, and brent geese often feed on intertidal mudflats and saltmarshes. (Vickery *et al.,* 1999).

The period of widespread concern amongst farmers is mid-winter to spring, when geese switch to feed upon growing cereals and grass. The spring use of grass, high in protein, is selected by geese to provide the birds with adequate nutrition in preparation for migration (McKay *et al.,* 1994; Prop *et al.,* 1998; Kirby *et al.,* 1999). Overgrazing during this period may reduce the vigour and production of sward growth (Patton & Frame, 1981). (The extent of grass yield loss due to (barnacle) geese grazing on Islay has been estimated through exclosure experiments as up to 82% (Percival & Houston, 1991).) Additionally, in areas of heavy goose grazing, yield losses of barley, wheat, straw and silage have been recorded (Patterson *et al.,* 1989; Patton & Frame, 1981; Vickery *et al,* 1999). Damage also includes 'puddling' of the land, whereby excessive trampling by large numbers of geese, coupled with heavy rainfall, compacts the soil structure, inhibiting drainage, which can reduce grass fields to mud mires that require subsequent ploughing and re-planting (Patton & Frame, 1981; Kirby *et al.*, 1999). Geese may also compete directly with livestock for grazing of spring pasture (Owen, 1990), and economic loss may be appreciable if alternative stock feed is needed (Patton & Frame, 1981).

Returning birds must be able to discern from memory the field sites where they benefited from minimal disturbance and forage of suitable nutritional composition in previous years, for geese display remarkable site fidelity in their choice of wintering location and the fields they forage in. Unfortunately, because large numbers of birds arrive within the span of a few weeks, the sudden arrival of perhaps several thousand birds often evokes a concerned response in landowners, irrespective of the actual damage that the birds may cause.

In addition, increased numbers of geese inevitably demand a greater foraging range. Birds may be gradually shifting away from traditional marginal wetland habitat and deeper into areas of agricultural importance. There is evidence that barnacle geese venture onto managed and heavily fertilised fields in preference to their traditional coastal feeding locations (Black *et al.*, 1991). Such factors combined alarm the farmers who only own small tracts of arable land, such as those on Islay, who face the arrival of over 40,000 barnacle geese every year (Kirby *et al.*, 1990), on an agricultural area of ca. 54 000 hectares (Patton & Frame, 1981), approximating to almost one goose/hectare.

Unfortunately, the combination of these factors often leads to concentrated numbers of geese affecting a few farms in areas close to roost sites. At present, farmers affected by goose damage are able to receive compensatory payments provided by the government based on projected yield losses. Such payment schemes are available in Canada, and are also established in the Netherlands (Kirby *et al.*, 1999). In Scotland, schemes have been set up to manage the problem of agricultural conflict, and award payments to farmers relating to the perceived risk of damage, whether or not damage occurs. Such schemes have so far proved highly expensive (Kirby *et al.*, 1999).

How is damage by geese assessed?

No single method is currently available to assess and predict the potential damage caused by geese grazing. The underlying problem is that it is easiest to measure goose damage when there is direct competition with the crop product/other agricultural interest. The longer the period between the grazing (damage) and the harvest, the more difficult it becomes to assess grazing damage. Also, it may be difficult to separate the damage that different goose species have caused as they may graze in mixed flocks (Van Eerden, 1990), which may complicate payment.

Methods used to assess the extent by which geese are using and damaging land have included measurement of changes in vegetation biomass, measuring differences in the chemical and nutritive composition of vegetation foliage, goose trampling estimations, incidence of weeds over time, and estimating goose use by counting faecal pellets (Abdul Jalil and Patterson, 1989; Summers, 1990). Radio-telemetry methods have been used to define the activity budgets of grazing geese, to evaluate the proportion of active time foraging (Percival & Evans, 1996). Sward clipping and the application of fertilisers have been used to simulate and predict the goose impact in order to make yield loss predictions,

and to advise management policymakers (Patton and Frame, 1981; Jalil and Patterson, 1989). Mathematical modelling has also been used to predict goose population size, local grazing pressure and yield losses (Kirby *et al.*, 1999).

General solutions to the conflict

Because geese feeding on agricultural land are considered both as pest species and of conservation interest it is complicated to realise a management system that satisfies both criteria.

There are obvious lethal methods that may be applied to local goose populations in an attempt to reduce potential damage. Licensed killing by shooting or poisoning may be effective against smaller populations. Culls of the birds during their vulnerable flightless stage of nesting may also contribute to reducing flock sizes, although this would involve considerable international co-operation with Governmental organisations of countries where birds nest during the summer.

Ingenious methods of scaring birds from crops and pasture have been used, although determined and varied application is needed for bird scarers to prove effective (Kear, 1990). Methods of scaring and repelling birds range from hanging plastic bags on fences to sophisticated audio-visual equipment (recordings of distress calls) and chemical repellents (Kear, 1990). Bird scarers have not proved tremendously cost-effective (Percival *et al.*, 1997), as geese will not be deterred if the agricultural land is sufficiently important to them, or if they are not physically harmed by the device, so develop no fear of the repellent. There is evidence that even shooting may serve only as a temporary repellent for whole flocks (Summers, 1990). Additionally, scaring may cause unintentional changes in site use: although returning geese do display site-fidelity in their choice of fields, repeated disturbance of such stimuli as shooting may shift the birds onto adjacent pasture, which might then be adopted as more favourable habitat (Ebbinge, 1991), perhaps resulting in further agricultural damage.

The establishment of specifically designed wildlife reserves in close proximity to potential problem areas may help to alleviate conflict between geese and farmers. Reseeding and applying fertiliser to protected areas has been successful in increasing goose grazing intensity (Percival, 1993). Of course, to be properly effective reserves must be suitably managed to both attract and maintain geese throughout the winter period, which is

complicated and potentially costly, requiring careful husbandry. There must be an understanding of the potential trade-offs of maximising food availability, whilst limiting the energetic costs and possible predation risks that may be incurred in travelling to a new site (Gill, 1996). Reserves need to be specific to the goose species present in the area requiring protection, and any seasonal influx of geese must not produce detrimental effects on other wildlife using the reserve. Ideally, the reserve should be carefully managed to encourage other wildlife species throughout the summer months when geese are not present, to be cost-effective, and to encourage green-tourism through human visitors (Vickery *et al.*, 1997). Any such protected areas should be located a considerable distance from human disturbance, to prevent the birds rejecting the site. In opposition to establishing reserves, there is the opinion that by creating safe havens for birds, larger flocks may be encouraged and individual survival probability improved, thereby proving counter-productive to the main problem of increased population sizes in geese (Owen, 1977).

There is evidence that geese are concentrating on 'improved' and heavily fertilised land (Owen, 1977). Encouraging arriving migrants to abandon their original sites in favour of new, specifically managed fields/sites may provide some grazing relief from privately owned pastureland (Vickery *et al.*, 1999). Of course, if the intention of the site is to attract problem birds from agricultural land, any alternative site should be located suitably close to the original agricultural sites, yet the new site must be substantially more appealing to the geese. Such an alternative may be problematic to create. Under private finance, such a scheme is unlikely to be adequately cost-effective over a long-term, due to the expenses involved in purchasing and maintaining suitable sites. There may also be high costs incurred initially in attempting to displace birds from their original sites by scaring (Percival *et al.*, 1997). However, European policy incentives encourage 'set-aside' of agricultural land, yet allow some fertiliser application to pastureland under certain 'flexible' schemes, which may encourage some landowners (Gill, 1996).

In conjunction with these methods of dispersal and control, it may be necessary for farm managers to begin to modify their field use. It may be appropriate to gradually change the location of vulnerable crops and pastureland so that they are planted close to roads or human habitation to discourage geese from establishing themselves on these prime sites. In addition, it may be effective to plant less palatable crop varieties in areas targeted by geese (Owen, 1990).

What solutions have been applied in Scotland?

Five goose control methods have been implemented in Scotland. In Islay, damages relating to barnacle and white-fronted geese are paid in cash as £9.50 for each goose that may present agricultural conflict. Such a scheme is enormously expensive, and has been criticised for being over-generous. In Orkney, a combination of scaring birds from agricultural areas, whilst providing them with alternative improved areas has proved highly economical (Kirby *et al.*, 1999). The Loch of Strathbeg (Aberdeenshire) scheme proved so highly successful in alleviating damage by pink-footed geese that it is no longer a problem in that area. Through this system of management farmers applied for compensation on the basis of analysis of goose use of the land through faecal pellet density estimates, and a projected economic impact from this information. The scheme also included scaring and offering improved pastureland (as for Orkney). The Uists scheme provides support in the form of advice to help farmers structure their own goose management schemes applying to Scottish greylag populations (Kirby *et al.*, 1999).

Conclusions

To be effective, any goose management strategy should:

- supply the appropriate habitat provision either for birds to reside the winter within, or as suitably tempting alternatives for birds displaced by scaring activities,
- serve to work in accordance with the current understanding of population distribution and dynamics,
- respect UK and International legislation and comply with any restrictions,
- regulate any shooting/hunting effectively to prevent irreversible damage to goose stocks.

Unfortunately, the monetary values of wildlife rarely equal agricultural rewards. In Canada, the value of waterfowl hunting and its associated activities is estimated at $1 billion/year (Canadian dollars) (Kirby *et al.*, 1999). The UK is yet to realise the potential revenue that could be acquired through managing its wild geese stock carefully for sporting purposes. Although a conservation conflict may develop through such management, it must be realised that by careful evaluation of the anticipated revenue in terms of managed shooting and green tourism (i.e. at specific sites); funds derived from regulated commercial hunting could contribute towards establishing long-term reserves for geese.

Other, non-lethal, systems of management also need further investigation to fully realise their effectiveness. No single management option will eliminate the potential problems caused by wintering geese, but by exploring and further evaluating various goose refuges and goose deterrent schemes for different species, a better understanding of how they should be implemented will develop. At present, a combination of strategies, specific to the species and agricultural issues of areas where conflict occurs provides the most effective solution.

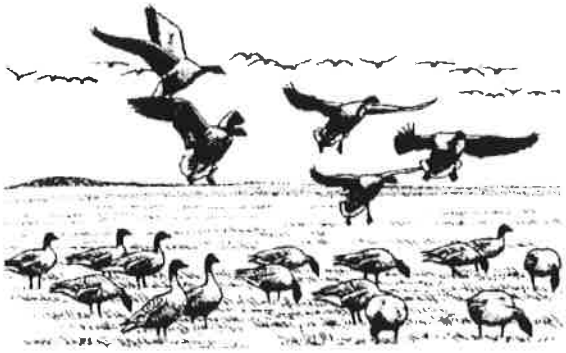

Illustration by Sir Peter Scott,
Reproduced from 'Wildfowl in Great Britain', (Owen *et al.*, 1986)

Appendix

Table 1. Reproduced from 'Geese and their interactions with agriculture and the environment' by Kirby JS, Owen M and Rowcliffe JM (1999).

Table 4.1 Maximum numbers[1], and the current trend in numbers, for the most significant goose populations of Scotland.

Population	Global Population	Numbers in Britain	Numbers in Scotland[2]	Numerical Trend
Icelandic Pink-footed Goose	235,000	235,000	235,000	Increasing
Icelandic Greylag Goose	80,000	80,000	80,000	Stable?
Greenland Barnacle Goose	45,000	37,000	37,000	Increasing
Svalbard Barnacle Goose	23,000	23,000	23,000	Increasing
Greenland White-fronted Goose	30,000	15,000	15,000	Increasing
Scottish Greylag Goose	10,000	10,000	10,000	Increasing
Bean Goose	80,000	450	135	Stable
TOTALS[3]	503,000	400,000	400,000	
Naturalised Greylag Goose	N/A	22,000	3,000	Increasing
Introduced Canada Goose	N/A	64,000	1,000	Increasing
GRAND TOTALS[4]	503,000	486,000	404,000	

1 Note that the numbers are derived from the population accounts presented in chapter 3 and have not been formally adopted by governmental or non-governmental organisations, *e.g.* for the purposes of site designation. They have been used here in preference to the figures of Stone *et al.* (1997) since those figures are based on data from the early 1990s, principally 1991 and 1992. Number rounded to nearest thousand.

2 Resident or spending part or the whole of the non-breeding season in Scotland.

3 Excluding naturalised and introduced populations.

4 Figure rounded

Table 2. Reproduced from Vickery and Gill, 1999.

Table 1
British wintering population size of species of wild migratory geese that cause agricultural conflict. Data for 1960–1980 are from Wildfowl and Wetlands Trust surveys (cited in Owen, 1990), 1990 data are from Kirby et al. (1991) and 1995 data are from Waters et al. (1996). Some of the counts for populations between 1960, 1970 and 1980 include a measure of estimation, which is based on data from adjacent years and/or known trends (see Owen, 1990). Figures for 1990 and 1995 are the maximum numbers recorded in any one month given to the nearest 1000 geese

	British population in				
Species	1960	1970	1980	1990	1995
Pink-footed goose	57,000	72,000	95,000	195,000	200,000
Greylag goose (Icelandic)	26,000	65,000	90,000	115,000	83,000
Greenland white-fronted goose	3000	2000	4000	15,000	22,000
Barnacle goose	5000	18,000	21,000	34,000	47,000
Dark-bellied brent goose	15,000	24,000	67,000	116,000	101,000
Total	106,000	181,000	277,000	475,000	453,000

Table 3. Reproduced from 'Geese and their interactions with agriculture and the environment' by Kirby JS, Owen M and Rowcliffe JM (1999).

Table 6.1 The status of the goose populations of Scotland under national and international legislation

Population	W&C Act 1981[1]	EU Birds Directive[2]	Berne Convention[3]	Bonn Convention
Icelandic pink-footed goose	Schedule 2, Part I	Annex II/2	Appendix III	Appendix II
Icelandic greylag goose	Schedule 2, Part I	Annex II/1, Annex III/2	Appendix III	Appendix II
Greenland barnacle goose	Unscheduled	Annex I	Appendix II	Appendix II
Svalbard barnacle goose	Unscheduled	Annex I	Appendix II	Appendix II
Greenland white-fronted goose	Unscheduled	Annex I Annex II/2	Appendix III	Appendix II
Scottish greylag goose[4]	Schedule 1, Part II Schedule 2, Part I	Annex II/1, Annex III/2	Appendix III	N/A
Naturalised greylag goose	Schedule 2, Part I	Annex II/1, Annex III/2	N/A	N/A
Bean goose	Unscheduled	Annex II/1	Appendix III	Appendix II
Introduced Canada goose	Schedule 2, Part I	Annex II/1	N/A	N/A

1 Schedule 2, Part I - may be killed or taken outside the close season
Unscheduled - fully protected at all times
Schedule 1, Part II - protected by special penalties during the close season
Close season is 1 February to 31 August, 21 February to 31 August below high-water mark of ordinary spring tides
No species may be sold

2 Annex I - "shall be *the subject of special conservation measures* concerning their habitat"
Annex II/1 - may be hunted throughout the EC
Annex II/2 - may be hunted in some EU member states
Annex III/2 - may be legally sold subject to consultation with the Commission

3 Appendix II - fully protected at all times
Appendix III - protected but may be subject to regulated exploitation

4 The Act does not explicitly recognise the "Scottish" greylag population. It gives special protection to greylag breeding in the "*Outer Hebrides, Caithness, Sutherland and Wester Ross only*". This is intended to protect the Scottish greylag population but individuals from the naturalised population, or indeed from the Icelandic population that chose to breed in these areas, would also thereby have specially protected status.

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