# Predation on seabird eggs by Keen's mice (*Peromyscus keeni*): using stable isotopes to decipher the diet of a terrestrial omnivore on a remote offshore island

**M.C. Drever, L.K. Blight, K.A. Hobson, and D.F. Bertram**

**Abstract**: We used stable isotope techniques to analyze tissues of Keen's mice (*Peromyscus keeni*) and Townsend's voles (*Microtus townsendii cowani*) and a subset of prey items at Triangle Island, British Columbia, western Canada's largest seabird colony. Isotope analysis allowed us to investigate the importance of seabird prey in rodent diets in a system where seabirds and non-introduced rodents occur sympatrically. The $\delta^{15}N$ values for terrestrial plants and terrestrial invertebrates on Triangle Island exceeded levels found in many terrestrial biomes and are typical of localities with high inputs of marine-derived N. We used multiple-source mixing models to estimate the relative inputs of potential prey items to vole and mouse diets. The $\delta^{13}C$ and $\delta^{15}N$ values of liver and muscle tissues of voles indicate that voles on Triangle Island derived their protein primarily from terrestrial plants, with some contribution by terrestrial invertebrates. In contrast, isotopic values of liver and muscle tissues of mice on Triangle Island indicated that mice prey primarily on seabird eggs and terrestrial invertebrates. Our results show that egg predation on Triangle Island is a general phenomenon in the mouse population, rather than occurring in only a few specialist feeders. Mice appear to feed on eggs once they become available and continue to utilize seabird prey, likely in the form of abandoned eggs or carcasses of chicks and adults, throughout the breeding season.

**Résumé** : Nous avons utilisé la technique des isotopes stables pour analyser les tissus de la Souris de Keen (*Peromyscus keeni*) et du Campagnol de Townsend (*Microtus townsendii cowani*) et ceux de plusieurs de leurs proies à l'île du Triangle, Colombie-Britannique, là où il y a la plus grande colonie d'oiseaux marins de l'Ouest canadien. L'analyse des isotopes nous a permis d'évaluer l'importance des oiseaux marins dans le régime alimentaire des rongeurs dans un système où les oiseaux marins et les rongeurs indigènes se retrouvent en sympatrie. Les valeurs de $\delta^{15}N$ pour les plantes terrestres et les invertébrés terrestres de l'île du Triangle excèdent les valeurs qui prévalent dans plusieurs biomes terrestres et sont typiques d'endroits où il y a un apport important d'azote d'origine marine. Nous utilisons des modèles de mixage de plusieurs sources pour estimer l'apport relatif des proies potentielles dans le régime des campagnols et des souris. Les valeurs de $\delta^{13}C$ et $\delta^{15}N$ des tissus hépatique et musculaire des campagnols indiquent que ceux-ci prennent leurs protéines surtout dans les plantes terrestres et un peu aussi dans les invertébrés terrestres. En revanche, les valeurs isotopiques des tissus hépatique et musculaire de la souris indiquent que les souris de l'île du Triangle consomment surtout des oeufs d'oiseaux marins et des invertébrés terrestres. Nos résultats indiquent que la prédation exercée sur les oeufs des oiseaux marins de l'île du Triangle est un phénomène généralisé dans la population de souris plutôt que l'apanage de quelques prédateurs spécialistes. Les souris semblent se nourrir d'oeufs dès que ceux-ci deviennent disponibles et ils continuent d'exercer leur prédation sur les oiseaux marins, probablement sous forme d'oeufs abandonnés ou de carcasses de jeunes ou d'adultes, pendant toute la saison de la reproduction.

[Traduit par la Rédaction]

## Introduction

Understanding factors that influence reproductive success in seabirds is crucial to developing predictive population models for management and conservation purposes. Variation in seabird reproductive success is controlled by several factors, including weather, predation risk, age and breeding experience of parents, and timing and quality of available

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**M.C. Drever.** Pacific Wildlife Research Centre, Canadian Wildlife Service, 5421 Robertson Road, R.R. No. 1, Delta, BC V4K 3N2, Canada.
**L.K. Blight.**[1] Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.
**K.A. Hobson.** Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, Saskatoon, SK S7N 0X4, Canada.
**D.F. Bertram.** Pacific Wildlife Research Centre, Canadian Wildlife Service, 5421 Robertson Road, R.R. No. 1, Delta, BC V4K 3N2, Canada, and Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

[1]Author to whom all correspondence should be addressed (e-mail: lkblight@sfu.ca).

food (Furness and Monaghan 1987). Depredation of eggs, adults, and young by introduced rodents, primarily rats (*Rattus* spp.), is well-recognized as playing a significant role in seabird breeding success (Moors and Atkinson 1984; Hobson et al. 1999). However, depredation by *native* rodents has largely been ignored despite the importance of understanding and quantifying the magnitude of such natural sources of mortality. The absence of native predators is thought to be important in the evolution of island nesting in seabirds (Furness and Monaghan 1987), and while localities where native rodents occur sympatrically with breeding seabirds appear to be rare, predation rates in these situations can be high. At Triangle Island, British Columbia, egg depredation by native Keen's mice (*Peromyscus keeni*; hereinafter referred to as mice) occurs in up to 30% of burrows of Cassin's auklets (*Ptychoramphus aleuticus*; Morbey 1995; D.F. Bertram, unpublished data) and in up to 34% of burrows of rhinoceros auklets (*Cerorhinca monocerata*; Blight et al. 1999). Native rodents also prey on seabird eggs elsewhere in the world. For example, Murray et al. (1983) reported that the eggs of Xantus' murrelets (*Synthliboramphus hypoleucus*) are depredated by deer mice (*Peromyscus maniculatus elusus*) on Santa Barbara Island, California. *Peromyscus* sp. also prey on eggs of the ancient murrelet (*Synthliboramphus antiquus*) at Haida Gwaii (Queen Charlotte Islands), British Columbia (Gaston 1992).

At Triangle Island, only two species of rodents occur: native mice (*P. keeni*) and an endemic race of Townsend's vole (*Microtus townsendii cowani*). Our study used stable isotope analysis to determine the relative importance of seabird eggs in the diet of rodents at this remote island colony. Traditional methods of diet analysis, such as analyses of stomach contents, have limited utility in determining a predator's consumption of eggs. Eggshells are not preserved well in stomach acid and egg yolk or albumen can be almost impossible to identify a few hours after their consumption (Duffy and Jackson 1986). Furthermore, single samples of stomach contents do not take seasonal dietary variation into account. Analysis of stable isotope ratios in tissues of predators circumvents this limitation, and when used appropriately it has several advantages (Hilderbrand et al. 1996; Hobson and Sealy 1991). The stable isotope approach provides information on diet integrated over various time scales, depending on the tissue chosen. For example, isotopic analyses of liver tissue provide information on food assimilation over a week, while analyses of muscle tissue provide information on diet over about a month (Tieszen et al. 1983; Hobson and Clark 1992). Thus, in contrast to conventional techniques, it is possible to derive information over ecologically relevant time periods, and specialists feeding exclusively on one or two prey types may be readily identified.

Because $\delta^{15}N$ analyses provide information on trophic level, whereas $\delta^{13}C$ analyses provide information primarily on the source of nutrients to the diet (Peterson and Fry 1987), the use of these two isotopes (or more) typically provides better resolution in tracing the diets of consumers and eliminates the ambiguities that accompany the use of a single isotopic tracer (Peterson et al. 1985). The ocean is generally enriched in $^{13}C$ relative to terrestrial ecosystems (Peterson and Fry 1987), and the relative abundance of $^{13}C$ remains comparatively unchanged with each trophic transfer (DeNiro and Epstein 1978; Schoeninger and DeNiro 1984). Thus, the measurement of $^{13}C$ can serve as a useful tracer of marine protein in the diet of animals (Hobson 1987; Hobson and Sealy 1991). Conversely, $\delta^{15}N$ values in marine and terrestrial organisms show a stepwise enrichment that is due to the preferential loss of the lighter isotope, $^{14}N$, during excretion (Peterson and Fry 1987) and serve as good indicators of trophic level of the sample organism (Minagawa and Wada 1984; Hobson et al. 1994). Stable N isotope ratios in marine systems may also be typically enriched compared with terrestrial food webs (Schoeninger and DeNiro 1984; Wada and Hattori 1991; Michener and Schell 1994).

Stable isotope analysis has recently been used at another seabird colony to examine diets of Norway rats (*Rattus norvegicus*) preying on ancient murrelets at Langara Island, British Columbia (Hobson et al. 1999). Murrelet eggs, chicks, and adults had stable isotope ratios greatly enriched in both $^{15}N$ and $^{13}C$ compared with other food types available, and this allowed a direct estimate of the proportion of the rat population feeding on seabirds. We predicted that rodents eating seabird eggs at Triangle Island would have tissues similarly enriched in both isotopes in contrast to tissues of those rodents eating exclusively plant-based diets. Our goals in using stable-isotope analysis were to ask (*i*) whether egg depredation at Triangle Island is the work of a few individuals specializing on seabird prey or is a general phenomenon among all mice and (*ii*) whether seabird eggs are also consumed by voles. Although egg and chick depredation by herbivorous voles do occur (Sealy 1982), it appears to be rare, and we hypothesized that it would be unlikely on Triangle Island. We also used stable-isotope analysis to ask (*iii*) whether rodent subpopulations showed dietary differences based upon season or locality.

## Study site and methods

### Study site

Our study took place from March to May 1997 and from April to August 1998, at Triangle Island, British Columbia (50°52′N, 129°05′W; 144 ha). Triangle Island is an ecological reserve that lies 46 km to the northwest of Cape Scott at the northern end of Vancouver Island, British Columbia, Canada. The island is western Canada's largest seabird colony and provides nesting habitat for 1.2 million birds of 12 species, primarily rhinoceros and Cassin's auklets (Rodway et al. 1990). Cassin's auklets begin arriving at the colony in March, and laying typically begins in that month. Rhinoceros auklets begin laying in mid to late April (L.K. Blight and Triangle Island Research Station, unpublished data). In 1997, our study focused on three localities: (*i*) West Bay, where Cassin's auklets nest at high density; (*ii*) Calamity Cove, where both Cassin's auklets and rhinoceros auklets nest in moderate densities; and (*iii*) South Bay – cabin site. Burrow density for rhinoceros auklets in South Bay is high, while Cassin's auklet burrows are found there in lower numbers (Rodway et al. 1990). In 1998, we established two study plots in South Bay. Plot 1 was situated approximately 30 m from 1997's cabin site, and plot 2 lay about 300 m to the east of plot 1.

### Sampling rodents and likely prey types

In early May 1997, we set snap traps within 50 m of the shore for two nights at two localities (West Bay, $n = 17$ traps; Calamity Cove, $n = 9$ traps). Traps were set 15 m apart under cover of vegetation or logs and were baited with peanut butter. Mice from the

cabin site were collected in March–April 1997, before most of the egg-laying activity began. These mice were trapped for routine hygiene measures or were found dead in the area. In 1998, permit restrictions precluded the use of snap traps. Instead, mice were trapped using Sherman live traps baited with peanut butter and euthanised using $CO_2$. Five mice were collected from each of our two study plots in South Bay between 31 May and 03 June (hereinafter referred to as early); another five mice were collected from each plot in the same manner on 22 August (hereinafter referred to as late). One mouse found dead in May in South Bay was added to the plot 1 (early) samples. As we did not receive permission to collect voles (red-listed in British Columbia), the samples that we analyzed were from three dead animals, salvaged from the three study localities over the months of April–June. All rodents were sexed, weighed, and measured and their reproductive state was recorded.

In 1998, we also carried out livetrapping in both South Bay study plots to estimate mouse population density. A total of 45 live traps (25 in plot 1 and 20 in plot 2) were placed on a grid pattern 10 m apart. Trapping was carried out over 3 nights between 28 May and 01 June, and for 3 nights between 30 June and 02 July. Trapping effort was suspended on rainy nights, and we excluded 30 June's trapping results for plot 2 from our analyses, owing to the high proportion (47%) of traps found tripped but empty on that night. Mouse collection was separated in time and (or) space from density estimate livetrapping in order not to confound our population estimates. We express all capture rates of mice in captures per 100 trap-nights (C/100 TN).

In 1997 and 1998, we also collected samples of prey representative of those available to mice and voles, including prevalent terrestrial plants, terrestrial invertebrates (1998 only), intertidal organisms, and abandoned (i.e., eggs found cold for ≥5 d) Cassin's auklet eggs (hereinafter referred to as CAAU eggs; 1997 only) and rhinoceros auklet eggs (hereinafter referred to as RHAU eggs). These items were not meant to exhaustively represent all food items available to mice and voles, but rather represented the broad categories of prey types found on the island.

## Isotopic analyses

Rodents were preserved in the field at –10°C in a propane freezer. Liver and muscle tissues were later sampled and freeze-dried, and ground into powder using a Wiggle-Bug dental amalgam mill (Crescent Dental Manufacturing, Lyons, Illinois, U.S.A.). Lipids were extracted via a chloroform–methanol rinse, as modified from Bligh and Dyer (1959), and samples were then loaded into tin cups and combusted at ~1800°C in a Europa Robo-Prep Elemental Analyzer, using a helium carrier gas interfaced with a Europa 2020 isotope ratio mass spectrometer (IRMS). This continuous flow IRMS technique provided $\delta^{15}N$ and $\delta^{13}C$ values with errors of ±0.2 and ±0.3‰ for C and N isotopes, respectively. Invertebrates of the same species were pooled and processed as one sample per species in each year of collection, so values of invertebrate samples represent a species mean. The standards used were PeeDee Belemnite for C and atmospheric air for N. All samples were analyzed at the Prairie and Northern Wildlife Research Centre and Department of Soil Science, University of Saskatchewan, Saskatoon.

The isotopic composition of any tissue is expressed as a ratio of the heavier to the lighter isotope relative to a standard. Commonly, δ notation of parts per thousand (‰) is used where

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

and $X$ is $^{13}C$ and $^{15}N$, and $R$ is the corresponding ratio $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Thus, tissues with larger $\delta X$ values are enriched with the heavier isotope relative to tissues with smaller $\delta X$ values.

## Statistical analyses of isotopic signals

We used a *k*-nearest neighbor randomization test to examine differences in $\delta^{15}N$ and $\delta^{13}C$ values among prey types (Rosing et al. 1998). This test treats $\delta^{15}N$ and $\delta^{13}C$ values as spatial data and calculates the probability that two observed samples are derived from the same population compared with the probability that samples with the same values were generated at random. We used 10 000 randomizations of the data to calculate probabilities. Using this approach ensured that prey types are bivariately and significantly different from each other (Ben-David et al. 1997*a*, 1997*b*), and thus enabled us to use dual-isotope, multiple-source mixing models to determine the relative contribution of each prey type to diets of rodents (see below).

We used multivariate analysis of variance (MANOVA) to test the null hypothesis of no differences among groups of rodents in $\delta^{15}N$ and $\delta^{13}C$ values of tissues and Tukey's multiple comparison tests to contrast levels where factors were significant at $\alpha \leq 0.05$ (Zar 1996). To avoid problems with the assumptions of multivariate normality and homogeneity of variances necessary for MANOVA, we used a permutation analysis to calculate the significance of Wilks' λ statistics (Hobson et al. 1999). We generated 10 000 permutations of the data, randomly assigning each bivariate point to a group of rodents. We then analyzed each permutation separately and compiled a randomization distribution of Wilks' λ statistics, and calculated the *P* value as the proportion of randomized values as extreme or more extreme than the observed value (Manly 1991).

We reasoned that the variance in isotopic signals for each group of rodents was analogous to inter-individual variance in diet. Thus, if rodents from one area had low variance, then we concluded that the group specialized in the same prey type(s). A group with a larger variance indicated a range of dietary strategies among individuals in that group.

## Multiple-source mixing model

To determine the relative contribution of each prey type to diets of individual mice, we used a multiple-source mixing model (Kline et al. 1990, 1993; Ben-David et al. 1997*a*, 1997*b*). This model uses the mean $\delta^{15}N$ and $\delta^{13}C$ values for each prey type (type A, B, C, etc.) corrected for the enrichment in the tissues of the consumer (i.e., the fractionation factor, A′, B′, C′; DeNiro and Epstein 1978, 1981; Tieszen et al. 1983). These corrected values represent the $\delta^{15}N$ and $\delta^{13}C$ values that would occur if the predator's diet consisted entirely of that prey type, and as the model uses means it does not place undue emphasis on any extreme values for a given prey type. We used a fractionation factor of +2‰ for C when eggs and plant matter were consumed and +1‰ when marine and terrestrial invertebrates were consumed, based on results from feeding experiments in captivity on mink and bears (Hilderbrand et al. 1996; Ben-David et al. 1997*a*, 1997*b*). We used a fractionation factor of +3‰ for $\delta^{15}N$ values of all prey types (DeNiro and Epstein 1981; Schoeninger and DeNiro 1984). The isotopic contribution of each prey type to the diet of each individual predator (P) is calculated as:

$$X_i = (1/PX')/(1/PA' + 1/PB' + 1/PC')$$

where $X'$ is A′, B′, or C′ and P$X'$ is the Euclidean distance ($z = (x^2 + y^2)^{1/2}$) between the $\delta^{15}N$ and $\delta^{13}C$ values of each predator (P) and the corrected prey types. The model assumes that individual predators consume all possible types of prey, and thus tends to overestimate the proportion of food types rarely consumed and underestimate the proportion of commonly used food items (Rosing et al. 1998). Therefore, the model provides indices of food consumption rather than actual proportions in the diet. We included all prey types (terrestrial plants, terrestrial invertebrates, intertidal organisms, RHAU eggs, and CAAU eggs) in examining the diet of mice from South Bay and Calamity Cove sites, but omitted RHAU eggs for mice from West Bay, since this prey type was not available at that locality.

**Table 1.** Morphometrics and population characteristics of Keen's mice (*Peromyscus keeni*) and Townsend's voles (*Microtus townsendii cowani*) from Triangle Island, British Columbia, 1997–1998.

| | | | Mass (g) | | Total length (cm) | | Tail to vent length (cm) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Dates of capture | *n* | Mean | SD | Mean | SD | Mean | SD | Sex ratio (males:females) | Proportion in breeding state |
| **Keen's mice** | | | | | | | | | | |
| South Bay | | | | | | | | | | |
| Cabin | 29 March – 2 April 1997 | 17 | 44.6 | 5.1 | 21.7 | 0.7 | 11.6 | 0.6 | 3.21:1 | 0.24 |
| Calamity Cove | 7 May 1997 | 7 | 49.6 | 5.5 | 22.4 | 0.9 | 11.7 | 0.4 | 2.5:1 | 0.57 |
| West Bay | 3 May 1997 | 9 | 48.4 | 6.5 | 22.0 | 0.6 | 11.4 | 0.4 | 2:1 | 0.67 |
| South Bay | | | | | | | | | | |
| Plot 1 (early) | 9 May, 31 May – 3 June 1998 | 6 | 38.8 | 7.1 | 20.9 | 2.8 | 11.1 | 2.4 | 0.2:1 | 0.50 |
| Plot 2 (early) | 3 June 1998 | 5 | 39.6 | 4.5 | 18.8 | 3.2 | 9.3 | 3.1 | 4:1 | 0.20 |
| Plot 1 (late) | 23 August 1998 | 5 | 49.2 | 4.5 | 21.6 | 1.5 | 11.1 | 0.8 | 0.6:1 | 0.00 |
| Plot 2 (late) | 23–24 August 1998 | 5 | 41.0 | 1.9 | 20.3 | 0.6 | 10.1 | 0.4 | 0.25:1 | 0.20 |
| **Townsend's voles** | 13 April – 29 June 1998 | 3 | 67.7 | 50.6 | 17.7 | 6.1 | 6.2 | 2.3 | 2:1 | 0.66 |

## Results

### Sample collection

In 1997, nine mice were captured in West Bay (52.9 C/100 TN), seven from Calamity Cove (77.8 C/100 TN), and 17 mice were obtained from the South Bay – cabin area over a 5-d period. In 1998, livetrapping for mouse density in South Bay yielded 64.4 C/100 TN for the May–June trapping and 58.9 C/100 TN for the June–July trapping. No voles were captured by our livetrapping effort. Rodent samples fell into eight groups based on species and location and time of capture: the three groups of mice captured in 1997 (South Bay – cabin, Calamity Cove, and West Bay), the four groups from 1998 (South Bay: plot 1 (early) and plot 2 (early); plot 1 (late) and plot 2 (late)), and the group of voles salvaged in 1998. Morphometrics and population characteristics are detailed in Table 1.

### Isotope analyses of prey types

Prey types differed primarily in their $\delta^{13}C$ values (Figs. 1 and 2).[2] Intertidal organisms were most enriched with $^{13}C$, followed by seabird eggs, terrestrial invertebrates, and terrestrial plants (Fig. 1). CAAU and RHAU eggs had similar $\delta^{13}C$ values (–19.9 and –20.2‰, respectively), but RHAU eggs were more enriched with $^{15}N$. The $\delta^{15}N$ values had similar means among prey types, and generally showed larger variance than $\delta^{13}C$ values (Fig. 2). Terrestrial invertebrates had the highest mean $\delta^{15}N$ value, although highest individual $\delta^{15}N$ values were found in terrestrial plants, particularly salmonberry (Fig. 1). Differences in mean $\delta^{13}C$ values provided good segregation among prey types. Stable isotope ratios differed significantly among prey types primarily because of differences in $\delta^{13}C$ values (*k*-nearest neighbor randomization test, $P < 0.001$ for all pairwise comparisons among prey types; Fig. 2), with the exception of terrestrial invertebrates (*k*-nearest neighbor randomization test, $P = 1.000$). This lack of difference, however, likely resulted from the small sample size ($n = 2$) for this prey type. Using the MANOVA and permutation analysis to calculate the *P* values (a procedure less conservative than the *k*-nearest neighbor randomization test), and Tukey's multiple comparison tests resulted in $\delta^{13}C$ values of terrestrial invertebrates differing significantly from all other prey types (Wilks' $\lambda = 0.073$, $P < 0.0001$, Tukey's multiple comparison test, $P < 0.05$).

### Isotope analyses of rodents

*Liver tissues*

Both $\delta^{15}N$ and $\delta^{13}C$ values of liver tissues, indicative of short-term diets of about 1 week, differed significantly among groups of rodents (Wilks' $\lambda = 0.230$, $P < 0.001$; Fig. 3).[3] Voles had liver tissues with $\delta^{13}C$ values similar to those of terrestrial plants, and which differed significantly from liver tissues of all mice groups (Tukey's multiple comparison test, $P < 0.05$). $\delta^{13}C$ values from liver tissues of mice were between $\delta^{13}C$ values of seabird eggs and terrestrial invertebrates and did not differ among mouse groups, with the following exception: $\delta^{13}C$ values of cabin mice liver tissues more closely resembled $\delta^{13}C$ values of intertidal organisms and had the greatest $^{13}C$ enrichment of mouse groups. Liver $\delta^{13}C$ values from cabin mice differed significantly from mice from Calamity Cove and the pooled August 1998 samples from South Bay (Tukey's multiple comparison test, $P < 0.05$; Fig. 3). Highest $\delta^{15}N$ values were found in vole liver tissues; these differed significantly from all mouse groups, except Calamity Cove. Calamity Cove mice had liver tissues with the highest $\delta^{15}N$ values of all mouse groups and differed significantly from $\delta^{15}N$ values of liver tissues from cabin mice

[2] Stable C and N isotope values for rodent prey types on Triangle Island, British Columbia, are archived at the NRC data depository. These data may be accessed by contacting the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada (telephone: 1-800-668-1222; e-mail: cisti.info@nrc.ca).

[3] Mean stable C and N isotope values for rodents' liver and muscle tissues at Triangle Island, British Columbia, are archived at the NRC data depository. These data may be accessed by contacting the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada (telephone: 1-800-668-1222; e-mail: cisti.info@nrc.ca).

**Fig. 1.** Stable C and N isotope values for prey types available to Keen's mice (*Peromyscus keeni*) and Townsend's voles (*Microtus townsendii cowani*) at Triangle Island, British Columbia. Terr. plants, terrestrial plants; Terr. inverts., terrestrial invertebrates; CAAU, Cassin's auklet eggs; RHAU, rhinoceros auklet eggs; and Intertidal, intertidal organisms.

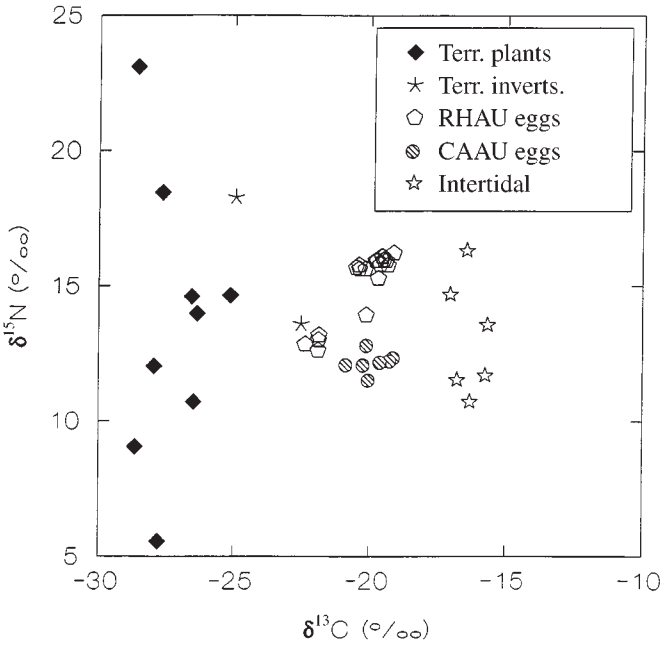
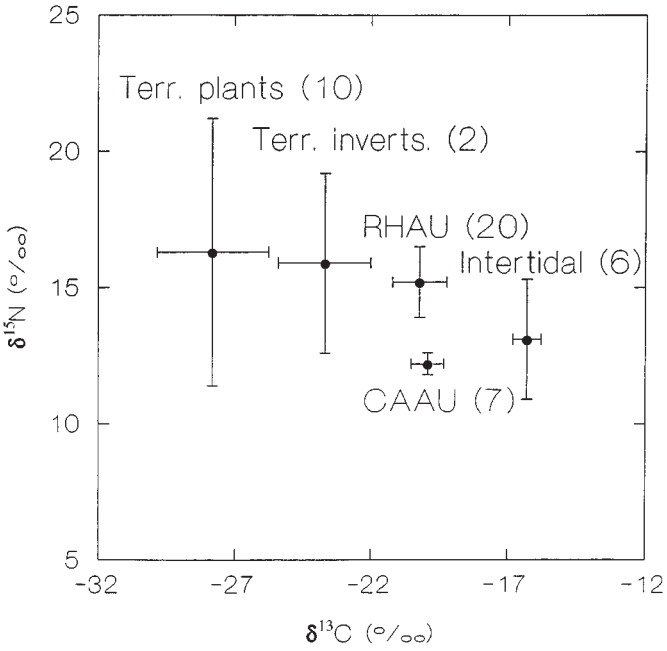


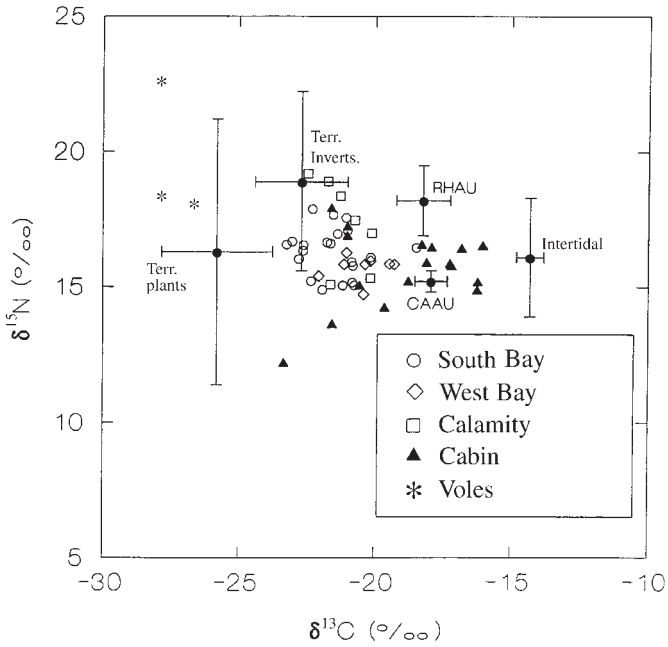

**Fig. 2.** Stable C and N isotope values (mean ± SE) for sample prey types. Numbers in parentheses are sample sizes. For abbrevation see Fig. 1.




(Tukey's multiple comparison test, $P < 0.05$), which had the lowest $\delta^{15}N$ values of all mouse groups. The remaining mouse groups all had liver tissues with similar $\delta^{15}N$ values (Tukey's multiple comparison test, $P > 0.05$; Fig. 3).

Mouse groups had coefficients of variance for liver $\delta^{13}C$ values that ranged from –2.3 to –6.5, with the exception of

**Fig. 3.** Stable C and N values (mean ± SE) in liver tissues of Keen's mice (*P. keeni*) and Townsend's voles (*M. t. cowani*) collected at Triangle Island, British Columbia, 1997–1998. Solid circles denote mean values (±SE) of possible prey types adjusted for fractionation effects. For the abbreviations see Fig. 1.



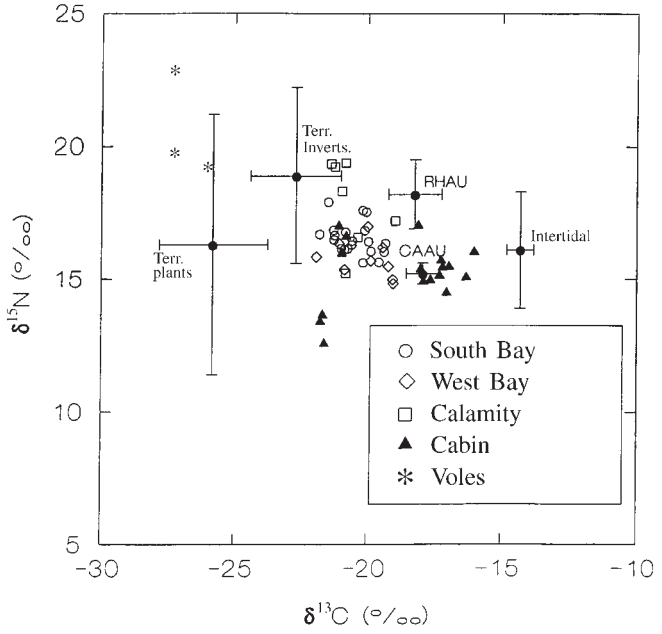

the cabin group, which had a coefficient of variance of –11.9, nearly double the largest value of other mice groups. Coefficients of variance for liver $\delta^{15}N$ values for South Bay and West Bay mice ranged from 2.9 to 4.9 and were lower than coefficients of variance for liver $\delta^{15}N$ values for voles and mice from the cabin and Calamity Cove, which ranged from 9.0 to 12.0.

*Muscle tissues*

The $\delta^{15}N$ and $\delta^{13}C$ values differed among groups of rodents (Wilks' $\lambda = 0.193$, $P < 0.001$; Fig. 4), and followed a similar pattern to $\delta^{15}N$ and $\delta^{13}C$ values in liver tissues. Voles had muscle tissues with the lowest $\delta^{13}C$ values, which differed significantly from muscle tissues of all mouse groups (Tukey's multiple comparison test, $P < 0.05$), and were similar to terrestrial plants (Fig. 4). Cabin mice had muscle tissues with $\delta^{13}C$ values more closely resembling $\delta^{13}C$ values of intertidal organisms (Fig. 4). These values were the highest of all rodents', and differed significantly from mice from Calamity Cove and the plot 1 (late) sample (Tukey's multiple comparison test, $P < 0.05$). The $\delta^{13}C$ values did not differ among muscle tissues of mice from West Bay, Calamity Cove, and the 1998 South Bay samples (Tukey's multiple comparison test, $P > 0.05$), all of which had $\delta^{13}C$ values between those of seabird eggs and terrestrial invertebrates.

Vole muscle tissues had the highest $\delta^{15}N$ values, and differed significantly from muscle tissues of all mice groups (Tukey's multiple comparison test, $P < 0.05$). Of the mice, Calamity Cove mice had the highest $\delta^{15}N$ values in muscle tissues and differed significantly from West Bay and cabin mice (Tukey's multiple comparison test, $P < 0.05$), which had the lowest $\delta^{15}N$ values. The 1998 South Bay samples

**Fig. 4.** Stable C and N values (mean ± SE) in muscle tissues of Keen's mice (*P. keeni*) and Townsend's voles (*M. t. cowani*) collected on Triangle Island, British Columbia, 1997–1998. Solid circles indicate mean values (±SE) of possible prey types adjusted for fractionation effects. For the abbreviations see Fig. 1.




had muscle tissues with intermediate $\delta^{15}N$ values and did not differ among each other and from the 1997 samples.

Coefficients of variance for muscle $\delta^{15}N$ and $\delta^{13}C$ values followed the same pattern as the liver tissues. Cabin mice had the largest variance of $\delta^{13}C$ values compared with other rodent groups. Coefficients of variance for muscle $\delta^{15}N$ values were similar among South Bay and West Bay mice but were lower than analogous values for voles and mice from the cabin and Calamity Cove.

### Multiple-source mixing model

The multiple-source mixing model indicated that the primary sources of protein for Keen's mice on Triangle Island were terrestrial invertebrates and CAAU and RHAU eggs, whereas terrestrial plants and intertidal organisms provided relatively less protein (Table 2). When considered together, CAAU and RHAU eggs provided the bulk of the protein (overall estimate is 51.0% for muscle and 43.0% for liver) in mouse tissues. RHAU and CAAU eggs provided similar amounts of protein in tissues for mice at sites where the two bird species occur together (19.0 and 20.0% for CAAU and RHAU eggs, respectively, at Calamity Cove; 21.0 and 20.0% at South Bay). The cabin group was an exception, where CAAU eggs appeared to be more important than RHAU eggs in diets of mice (Table 2). This was probably due to the early date of collection of these animals, as Cassin's auklets begin laying before rhinoceros auklets. In addition, the CAAU eggs prey type had a larger variance relative to the other prey types for mice in the cabin group, particularly in muscle tissues (Table 2). Little difference existed in the relative contribution of seabird eggs in diets of mice between the early South Bay samples and the late South Bay samples. In contrast to the mice, voles on Triangle Island derived their protein primarily from terrestrial plants (32.0 and 39.0% for muscle and liver tissues, respectively), followed by terrestrial invertebrates (30.0 and 25.0%; Table 2). The multiple-source mixing model estimated that seabird eggs and intertidal organisms provided relatively less protein for voles, but as the model forces all prey types to be considered, it presumably overestimated the contribution of these two prey types.

## Discussion

### Isotope analyses of prey types

Triangle Island is a varied isotopic environment, in which terrestrial, intertidal, and pelagic elements provide omnivorous rodents with a wide range of isotopic inputs. The $\delta^{15}N$ values for terrestrial plants and invertebrates on Triangle Island certainly exceeded levels found in many terrestrial biomes and are typical of places with high inputs of marine-derived N. These include other seabird colonies (Mizutani and Wada 1988; Cocks et al. 1998; Wainright et al. 1998), otter latrines (Ben-David et al. 1998), and salmon spawning grounds (Kline et al. 1990, 1993). Salmonberry provides a dramatic example: on Triangle Island, salmonberry had a mean $\delta^{15}N$ value of 15.3‰, whereas in southeast Alaska, salmonberry had a $\delta^{15}N$ value of 1.1‰ at sites with no contribution of marine-derived N (Ben-David et al. 1998). Terrestrial plants that do not fix N typically have $\delta^{15}N$ values that range from –8 to 10‰, depending on the isotopic composition of their soils (Peterson and Fry 1987). The highly enriched $\delta^{15}N$ values of plants on Triangle Island likely resulted from N uptake from soils enriched in $^{15}N$, owing to incoming marine-derived N in seabird guano and by the process of volatilization of isotopically light ammonia from the guano (Mizutani et al. 1986; Mizutani and Wada 1988). In this situation, where two very different biomes (i.e., marine and nonmarine) contribute to nutrient input, $^{15}N$ serves as a useful tracer of nutrient source but loses its utility as a straightforward indicator of trophic level. On Triangle Island, mice and voles feeding on primary producers (terrestrial plants) had higher $\delta^{15}N$ values than rodents feeding at higher trophic levels. In studies using stable isotopes, characterizing $\delta^{15}N$ values of available food sources is required before inferences about the trophic level of a consumer can be made (Hobson 1999).

Intertidal organisms were more enriched in $^{13}C$ than seabird eggs, a pattern that reflects the gradient of decreasing abundance of $^{13}C$ in the ocean from the intertidal to the pelagic zone (France 1995). Similarly, Hobson (1993) found that benthic-feeding seabirds had tissues more enriched in $^{13}C$ than those from pelagic seabirds. Although we could not use $\delta^{15}N$ values to predict the rodent trophic level at Triangle Island, stable N isotopes reliably predict seabird trophic positions, since their diets are strictly marine in origin (Hobson et al. 1994); the difference we observed between $\delta^{15}N$ values of RHAU eggs and CAAU eggs reflect dietary differences between the two seabird species (Hobson 1991). Rhinoceros auklets primarily eat fish, while Cassin's auklets typically feed on plankton (Gaston et al. 1998), and thus have lower $\delta^{15}N$ values in their eggs.

**Table 2.** Relative contributions (%) of prey types to diet of Keen's mice (*P. keeni*) and Townsend's voles (*M. t. cowani*) on Triangle Island, British Columbia (1997–1998), estimated using a multiple-source mixing model with isotopic data from two tissues.

| | | CAAU eggs | | RHAU eggs | | Intertidal organisms | | Terrestrial plants | | Terrestrial invertebrates | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| **Liver tissues** | | | | | | | | | | | |
| Keen's mice | | | | | | | | | | | |
| South Bay | | | | | | | | | | | |
| Cabin | 17 | 36 | 14 | 21 | 4 | 17 | 8 | 11 | 6 | 15 | 10 |
| Calamity Cove | 7 | 19 | 10 | 20 | 8 | 10 | 3 | 13 | 4 | 38 | 22 |
| West Bay | 8 | 40 | 10 | 0 | — | 16 | 1 | 19 | 5 | 25 | 6 |
| South Bay | | | | | | | | | | | |
| Plot 1 (early) | 6 | 23 | 10 | 22 | 6 | 11 | 2 | 14 | 3 | 30 | 16 |
| Plot 2 (early) | 5 | 24 | 5 | 22 | 2 | 12 | 1 | 17 | 2 | 25 | 6 |
| Plot 1 (late) | 5 | 16 | 1 | 18 | 4 | 10 | 1 | 24 | 6 | 32 | 2 |
| Plot 2 (late) | 5 | 21 | 6 | 19 | 2 | 11 | 2 | 22 | 5 | 27 | 6 |
| Townsend's voles | 3 | 13 | 2 | 14 | 3 | 9 | 2 | 39 | 10 | 25 | 3 |
| **Muscle tissues** | | | | | | | | | | | |
| Keen's mice | | | | | | | | | | | |
| South Bay | | | | | | | | | | | |
| Cabin | 17 | 44 | 22 | 18 | 8 | 15 | 8 | 10 | 7 | 12 | 8 |
| Calamity Cove | 7 | 19 | 7 | 26 | 8 | 10 | 2 | 13 | 3 | 32 | 13 |
| West Bay | 9 | 45 | 14 | 0 | — | 16 | 1 | 16 | 6 | 23 | 8 |
| South Bay | | | | | | | | | | | |
| Plot 1 (early) | 6 | 29 | 12 | 23 | 4 | 12 | 1 | 13 | 2 | 23 | 11 |
| Plot 2 (early) | 5 | 31 | 6 | 28 | 4 | 12 | 1 | 11 | 1 | 18 | 3 |
| Plot 1 (late) | 5 | 21 | 2 | 24 | 5 | 11 | 1 | 16 | 3 | 28 | 3 |
| Plot 2 (late) | 5 | 25 | 4 | 24 | 2 | 12 | 1 | 15 | 2 | 24 | 5 |
| Townsend's voles | 3 | 13 | 2 | 15 | 2 | 10 | 2 | 32 | 5 | 30 | 2 |

**Note:** Refer to Table 1 for an explanation of early and late, which pertains to the capture dates of Keen's mice and Townsend's voles. CAAU, Cassin's auklet eggs and RHAU, rhinoceros auklet eggs.

### Seabird eggs and rodents on Triangle Island

The $\delta^{13}C$ values and the multiple-source mixing model indicated that mice on Triangle Island derive the bulk of their protein firstly from seabird eggs and secondly from terrestrial invertebrates. However, as plant prey (low protein) typically enters energy metabolic pathways, and animal prey (high protein) is a primary source of tissue synthesis in consumers (Gannes et al. 1997; Hobson and Stirling 1997), our estimates of protein contribution are greater than the actual proportion of a prey item in a rodent's diet. In contrast to mice, vole tissues have $\delta^{13}C$ and $\delta^{15}N$ values indicative of a largely terrestrial diet, with little marine input. This indication is supported by the model and by observations of voles on Triangle Island feeding exclusively on terrestrial plants (L.K. Blight, personal observation). Voles (*Microtus* sp. and (or) *Clethrionomys* sp.) on St. Lawrence Island, Bering Sea, have been observed eating eggs and nestlings of nesting auklets (Sealy 1982), although voles elsewhere are largely herbivorous and consume only small amounts (<10%) of animal protein, in the form of arthropods (Batzli 1985).

The importance of seabird eggs in diets of mice varied with time of year and locality at Triangle Island. The $\delta^{13}C$ and $\delta^{15}N$ values suggest that when eggs become available, predation on seabird eggs is not the work of specialist mice but rather is a general phenomenon in the mouse population, despite local variation in diet. The cabin mice were captured in early spring before the majority of seabirds begin breeding, although some early nesting activity by Cassin's auklets at that time is likely. These mice then represent mice that are least affected by breeding bird activity in the sampled years. The $\delta^{13}C$ and $\delta^{15}N$ values for the cabin group have larger variance than other mice groups, indicative of a more diverse diet that includes marine invertebrates. However, some of these mice may also have had access to particles of human food from dishwater disposed of on the beach. Stable C isotope ratios of mice from Calamity Cove, West Bay, and South Bay (early), trapped in the middle of the seabird breeding season, had a smaller variance than the mice trapped in March, suggesting that at this time of year mice have a smaller dietary breadth and may focus on seabird eggs when they become available. Such a phenomenon occurred at Langara Island, where isotopic signals of rats feeding on eggs and birds in the ancient murrelet colony had much smaller variances than signals of rats collected elsewhere on the island. Since rat $\delta^{15}N$ and $\delta^{13}C$ values were similar to $\delta^{15}N$ and $\delta^{13}C$ values of ancient murrelet tissues, the small variance indicated that rats fed on murrelets almost exclusively (Drever and Harestad 1998; Hobson et al. 1999). Similarly, rats raised on monotonous diets in the laboratory showed minimal variance in bone collagen $\delta^{13}C$ values (Ambrose and Norr 1993; although collagen is expected to have lower variance as it represents a much longer-term integration of diet than muscle or liver). Mice sampled by us in South Bay showed little difference between early (May–June) and late

(August) samples. Although seabirds have finished incubating by the latter date, this lack of difference suggests that mice continue to feed on seabird prey, as abandoned eggs and carcasses of chicks and adults remain available into the late summer.

**Implications for rodent populations**

The acquisition of protein is crucial for growth, survival, maintenance, and reproduction. Seabird eggs likely provide the bulk of the input of protein for mouse tissues on Triangle Island, yet are available only as a seasonal influx of nutrients. It has been proposed that reduced food availability over the winter months is the limiting factor for mouse populations at Triangle Island (Carl et al. 1951). We suggest that mice there synchronize their breeding efforts to this influx of avian food, particularly as availability of seabird eggs precedes that of seeds and invertebrates. Island populations of rodents typically have distinct, short reproductive seasons (Gliwicz 1980; Adler and Levins 1994) and rodent populations often eat more animal prey when breeding relative to other times (Clark 1981).

We also suggest that seabird presence may account for the exceptionally high density of mice on Triangle Island. In a study where rodents were trapped at 46 islands in southern British Columbia, the average trapping sucess was 28.2% for islands where mice (*Peromyscus maniculatus*) were present. No islands under 25 ha ($n$ = 16) had a population of mice, with the exception of Mandarte Island (5 ha), the only seabird colony sampled; trapping success there was 73.8% (Redfield 1976). The Mandarte Island values compare with a mean trapping success of 63.5% at Triangle Island. Availability of seabird prey may also account for the sympatry of mice and voles on our study island; Redfield (1976) found only one island where *Microtus townsendii* occurred, and that was at an island where *Peromyscus maniculatus* was absent, likely because of competitive exclusion.

In 1997, the March–April sample of mice from the South Bay – cabin site had the smallest proportion of breeding individuals and the later samples from West Bay and Calamity Cove contained larger proportions of breeding individuals. In 1998, juvenile mice were virtually absent from the May–June livetrapping but comprised the bulk of the animals trapped in June–July (L.K. Blight, unpublished data). While our sampling scheme partially confounds time with location, this concurrence of breeding effort and high seabird egg contribution to mouse diet suggests that mice at Triangle Island time their breeding to coincide with the laying season of Cassin's and rhinoceros auklets, when a large influx of protein-rich food becomes available.

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