

Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis

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Abstract

The presence of introduced Norway rats *Rattus norvegicus* has raised concerns for the fate of the large least auklet *Aethia pusilla* colony situated at Sirius Point, Kiska Island, Alaska. Previous studies have documented extreme interannual variation in least auklet reproductive success and potential drastic population declines, both of which have been attributed to the varying abundance of, and predation by, Norway rats. A diet study would resolve the uncertainty that remains about the role of rats in the auklet's reproductive failure and the colony's decline. Our main objectives here were to quantify the variation in diet of introduced Norway rats and assess predation on least auklets. Using stable isotope analysis we document wide variability in rat diet dependent on location and provide direct evidence that Norway rats are preferentially preying on least auklets at Sirius Point. In conclusion, we hypothesize that the observed wide variability in rat diet will contribute to the persistence of rats on Kiska long after auklets have been extirpated. The persistence of rats enabled by their foraging plasticity will increase their effects by creating ecological traps within which prospecting individuals will fall and be depredated. This has large conservation consequences as it suggests that when seabirds are extirpated recolonization by prospecting birds is virtually impossible and island ecosystems will continue to be negatively affected and altered as long as introduced predators, such as rats, remain within them.

Introduction

Introduced predators are a significant threat to island bird populations (Atkinson, 1985). For example, the dark-rumped petrel *Pterodroma phaeopygia* in Hawaii and the Galapagos Islands is threatened with extinction (Harris, 1970; Coulter, 1984; Harrison, Naughton & Fefer, 1984) and the Guadalupe storm-petrel *Oceanodroma macrodactyla* (Jehl & Everett, 1985; McChesney & Tershy, 1998) is now extinct, both because of introduced predators. For conservation purposes the quantification of ecological relationships, especially prey selection by such predators, is a critical first step in the design of mitigation plans. Nevertheless, while anecdotal information on predation is usually easy to obtain, measuring the actual number of prey taken by individuals and the importance of alternative food sources is often more difficult, especially for nocturnally active and subterranean predators such as Norway rats *Rattus norvegicus*.

The least auklet *Aethia pusilla* breeding colony at Sirius Point, Kiska Island, Alaska (52°N, 177°E; Fig. 1) is one of the largest auklet colonies in Alaska (G. V. Byrd, pers. comm.) and is likely experiencing a population decline due to introduced Norway rats (Major & Jones, 2005). Although there is considerable indirect evidence for a large impact of

rats on auklets, there is little direct evidence of the prevalence of auklets in rat diet at Sirius Point (Major & Jones, 2005; Major *et al.*, 2006). In order to quantify direct rat predation on auklets, we used stable isotope analysis (SIA) to assess the diet of rats at the auklet breeding colony and further investigate variations in rat diet across Kiska Island, a c. 40-km-long island with a variety of wetland and upland habitats.

SIA is used in ecology to reconstruct the diet and trophic level of many organisms (Hobson & Sealy, 1991), including insular rodent populations (e.g. Hobson, Drever & Kaiser, 1999; Drever *et al.*, 2000; Stapp, 2002). This is achieved because the isotopic ratios of a consumer are related to those of its food source in a predictable manner (DeNiro & Epstein, 1978, 1981). The ratios of stable isotopes of carbon and nitrogen ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ or $\delta^{15}\text{N}$) are often used to infer whether the protein in the diet of an animal is derived from a marine or a terrestrial source and the trophic level of the consumer, respectively (Hobson, 1987, 1990; Hobson & Sealy, 1991).

The objectives of this study were to quantify the variation in diet of introduced Norway rats and assess predation on least auklets. We hypothesized that as generalist predators rats will change diet with location to whatever the most

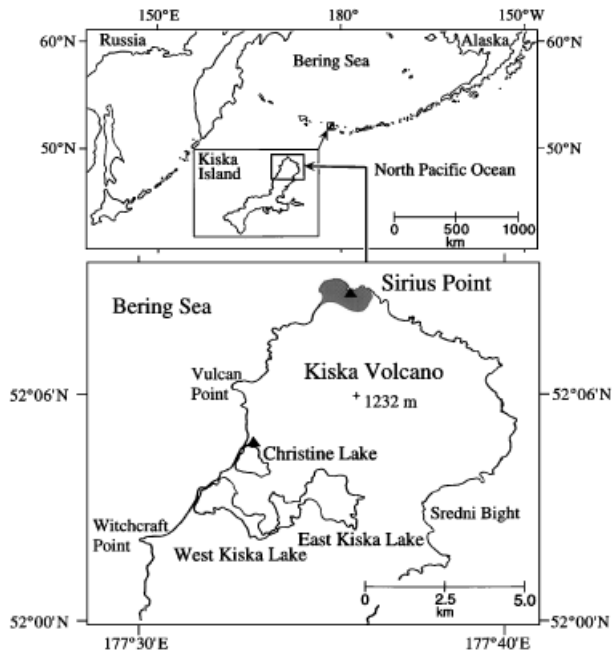


Figure 1 Map of the North Pacific and Bering Sea showing the location of Kiska Island, with an inset showing the locations of Sirius Point (auklet colony highlighted in grey), Christine Lake and East Kiska Lake.

readily available and highest nutritional quality prey may be, as suggested by Drever & Harestad (1998). In particular, we hypothesize that rats at Sirius Point will feed preferentially on least auklets.

Materials and methods

Study site

Our research was undertaken at Kiska Island (52°N, 177°E; Fig. 1), part of the Alaska Maritime National Wildlife Refuge (AMNWR). Kiska is the second largest island in the Rat Islands group in the western Aleutian Islands, Alaska, USA, is 39.8 km long and varies in width from 2.8 to 11 km, with a total area of 28 177 ha. Kiska Island is a remote treeless oceanic island, lying more than 800 km from the nearest continental land masses, with wet meadows of grasses (*Elymus arenarius*, *Calamagrostis* spp., *Poa* spp.), umbellifers (*Heracleum lanatum*, *Angelica lucida*) and various fern species in low-lying areas, alpine heaths in higher inland areas, and sparse to no vegetation at higher elevations and on recent lava flows and domes. At Sirius Point (52°08'N, 177°37'E) a large least and crested *Aethia cristatella* auklet colony is situated on two lava domes located at the base of the north slope of Kiska Volcano. The auklet colony occupies a surface area of c. 1.8 km² and hosted more than 1 million breeding least auklets in 2001 (I. L. Jones, unpubl. data).

Norway rat collection

We collected 40 Norway rats using snap traps at both Sirius Point (auklet colony, $n = 20$, 52°08.013', 177°35.854'; Fig. 1) and Christine Lake (brackish lagoon with access to nearby intertidal zone, $n = 20$, 52°05.004', 177°33.072'; Fig. 1) in each of 2002 and 2003. Collections began over a month after the arrival of auklets at Sirius Point and continued until our departure from Kiska in early August, ensuring an auklet signature would be present in both pectoral muscle (turn-over time of 1 month) and liver tissue (turnover time of 1 week) of Norway rats if they were being consumed. At Sirius Point we used unbaited traps placed along visibly used rat trails in grassy areas because rats were not attracted to bait. At Christine Lake rats were trapped with nearly 100% (per night) trapping success using traps baited with the fresh flesh of Dolly Varden *Salvelinus malma* from the lake. Using traps baited with the Dolly Varden, canned mussels and peanut butter, we trapped a total of 12 rats at East Kiska Lake (2.5 km inland, at 52°04.459', 177°35.011'; Fig. 1) in 2003 and 2004. Liver and pectoral muscle tissue samples were taken from each rat killed. In addition, we opportunistically sampled potential rat prey items at both Sirius Point and Christine Lake, including amphipods, Dolly Varden, freshwater algae, and liver and pectoral muscle from 20 adult least auklets and 10 adult crested auklets found freshly dead on the auklet colony. All samples were analysed in order to assess rat diet across Kiska Island.

SIA

We dried all isotope samples in an oven immediately after sampling for 3 h at 60 °C and then stored them in o-ring vials while in the field. Once in the lab we crushed and removed lipids from all isotope samples using a 2 chloroform:1 methanol rinse as modified from the Bligh & Dyer (1959) method. By removing lipids we were able to compare ingested protein (i.e. nutrients) but not fats. Once lipids were removed, we dried the samples in a drying oven at 60 °C (3–4 h), powdered and stored them in glass vials until analysis.

Our samples were analysed at the Stable Isotope in Nature Laboratory (SINLAB) at the University of New Brunswick. We loaded c. 0.2 mg of dried, powdered sample into tin capsules and burned them in a Carlo Erba NC2500 elemental analyzer (CE Instruments, Milan, Italy); resultant gases were delivered via continuous flow to a Finnigan Mat Delta XP mass spectrometer (Thermo Finnigan, Bremen, Germany). Our isotope ratios are reported relative to international standards for carbon [Peedee belemnite carbonate (PDB)] and nitrogen (atmospheric N₂, AIR) according to $\delta X = R_{\text{sample}}/R_{\text{standard}}$, where R is the ratio of heavy to light isotopes (e.g. ¹³C/¹²C) and X is the heavier isotope. We corrected our isotope values using International Atomic Energy Agency (IAEA) standards CH6 (−10.4 ± 0.1‰ SD and −10.4 ± 0.4‰ SD), CH7 (−31.8 ± 0.1‰ SD and −31.8 ± 0.2‰ SD), N1 (0.4 ± 0.2‰ SD and 0.4 ± 0.2‰ SD) and N2 (20.3 ± 0.1‰ SD and 20.3 ± 0.2‰ SD). One standard

deviation of sample repeats within a run was never greater than 0.34‰ for $\delta^{13}\text{C}$ and 0.64‰ for $\delta^{15}\text{N}$, and an internal lab standard (bovine liver) yielded values of $-18.7 \pm 0.08\%$ SD and $-18.8 \pm 0.2\%$ SD ($\delta^{13}\text{C}$) and $7.2 \pm 0.2\%$ SD and $7.3 \pm 0.1\%$ SD ($\delta^{15}\text{N}$) during sample analysis.

Change in rat diet across habitats

To assess differences in the feeding ecology of Norway rats across habitats, we compared rat isotopic signatures from liver and pectoral muscle tissues at three distinct locations at Kiska Island (the Sirius Point auklet colony, the intertidal and brackish water lake system of Christine Lake, and the freshwater and inland area of East Kiska Lake; Fig. 1) using multivariate analysis of variance (MANOVA; Wilks' Λ).

Multiple-source mixing model

To resolve variations in the diet of Norway rats at Kiska and determine the relative importance of least auklets in their diet at Sirius Point, we used the Visual Basic program Isosource to construct a multiple-source mixing model (Phillips & Gregg, 2003). We ran three mixing models, one for each location, using only those prey items available in each location. Least and crested auklets were only included in the model at Sirius Point as this is the only location where they are available. Dolly Varden and freshwater algae were included in the models for Christine and East Kiska Lakes only as they are not available at Sirius Point. Although we attempted to collect samples of all potential prey items, we did not have samples of terrestrial and marine vegetation. To obtain these values we constructed general $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the literature (Table 1).

In order to correct for the biochemical components of food change when incorporated into the tissues of a consumer, we applied a discrimination factor of 2‰ for plant matter and 1‰ for invertebrate, auklet and fish samples for carbon and 3‰ for nitrogen to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (DeNiro & Epstein, 1978, 1981; Tieszen *et al.*, 1983; Minagawa & Wada, 1984; Schoeninger & DeNiro, 1984). At Sirius Point, Norway rats predominantly eat brain tissue from auklets (H. L. Major & I. L. Jones, pers. obs.). To account for the biochemical differences between the sampled liver and muscle tissue to the consumed brain tissue, we used discrimination factors found by Mizutani, Kabaya & Wada (1991) for cormorant tissues. Using these values we converted our least and crested auklet samples from liver and muscle tissue to diet and then to brain tissue.

Table 1 General stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for terrestrial and marine vegetation as indicated in the literature

Potential prey item	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Source
Terrestrial	-27.000	0.100	Stapp (2002); Kelly (2000);
vegetation			Elder <i>et al.</i> (2000); Hobson, McLellan & Woods (2000)
Marine	-16.900	7.700	Davenport & Bax (2002);
vegetation			Rogers (2003); Stapp (2002)

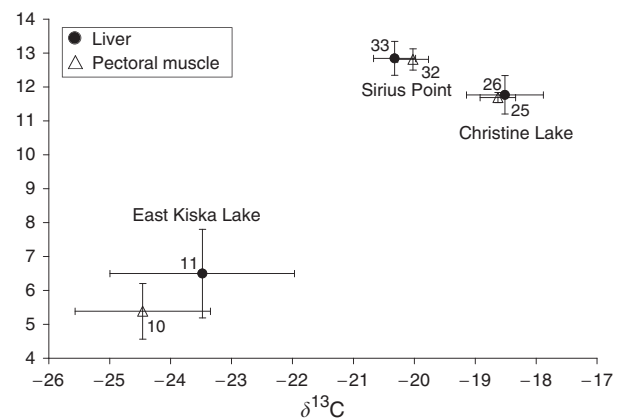


Figure 2 Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (shown as mean with 95% confidence interval and sample size) for pectoral muscle and liver tissue of Norway rats from Sirius Point, Christine Lake and East Kiska Lake, Kiska Island, Alaska.

Results

We measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from 78 lipid-extracted Norway rat liver samples from Sirius Point ($n = 36$), Christine Lake ($n = 30$) and East Kiska Lake ($n = 12$). Seventy-one lipid-extracted Norway rat pectoral muscle samples were measured from Sirius Point ($n = 34$), Christine Lake ($n = 27$) and East Kiska Lake ($n = 10$), and 20 least auklet liver and pectoral muscle samples came from Sirius Point only.

Change in rat diet across habitats

Statistical analysis (MANOVA) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of both liver tissue and pectoral muscle values revealed significant differences in Norway rat diet between the three locations (liver: Wilks' $\Lambda = 0.18$, $F = 50.04$, d.f. = 4, 148, $P < 0.001$; pectoral muscle: Wilks' $\Lambda = 0.04$, $F = 140.28$, d.f. = 4, 134, $P < 0.001$). Graphical examination of these results demonstrates these large differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among Sirius Point, Christine Lake and East Kiska Lake (Fig. 2). In particular, our results revealed that rats at Sirius Point foraged at the highest trophic level, closely followed by rats at Christine Lake, and those at East Kiska Lake foraged at a relatively low trophic level. Rats at Sirius Point and Christine Lake differed more in their carbon isotopic signature than in nitrogen, with the Christine Lake rats averaging nearly 2‰ higher in $\delta^{13}\text{C}$ (Fig. 2). Differences in $\delta^{13}\text{C}$ among the three sites revealed a marine signature (-21% , range = -18 to -24%) at Sirius Point and Christine Lake and a terrestrial signature (-27% , range = -35 to -21%) at East Kiska Lake (Fry & Sherr, 1989; Kelly, 2000).

Multiple-source mixing model

Our multiple-source mixing model revealed wide variability in rat diet dependent upon location. At East Kiska Lake rats obtain their protein predominantly from terrestrial vegetation whereas rats at Christine Lake obtain their protein

Table 2 Relative contributions (%) of prey types of Norway rats *Rattus norvegicus* at Kiska Island, Alaska, estimated using a multiple-source mixing model with isotope data from two tissues

	n	Mean (sd) range							
		Terrestrial		Marine		Freshwater algae	Dolly Varden	Crested auklet	Least auklet
		Vegetation	Invertebrates	Vegetation	Invertebrates				
Liver									
Sirius Point	36	4 (0.034) 0–15	62 (0.076) 47–86	4 (0.034) 0–18	2 (0.15) 0–8			17 (0.092) 0–40	11 (0.089) 0–50
Christine Lake	30	15 (0.031) 6–25	13 (0.10) 0–52	19 (0.085) 0–39	24 (0.190) 0–89	17 (0.133) 0–68	11 (0.088) 0–45		
East Kiska Lake	12	69 (0.040) 60–79	6 (0.046) 0–21			8 (0.064) 0–27	17 (0.073) 0–33		
Pectoral muscle									
Sirius Point	34	3 (0.025) 0–11	59 (0.082) 42–86	3 (0.025) 0–13	8 (0.055) 0.28			13 (0.084) 0–36	14 (0.106) 0–49
Christine Lake	27	16 (0.031) 7–26	13 (0.102) 0–52	19 (0.085) 0–39	24 (0.190) 0–89	17 (0.133) 0–68	11 (0.088) 0–45		
East Kiska Lake	10	79 (0.042) 70–90	6 (0.050) 0.23			6 (0.043) 0–19	9 (0.057) 0–26		

from the whole range of potential prey items sampled (Table 2). At Sirius Point rats obtain their protein mainly from terrestrial invertebrates but also prey upon both least and crested auklets (Table 2).

Discussion

Auklet colony implications

Previous studies at Kiska Island have shown that rats are similarly abundant in all regions where marine sources of prey are available, and the presence of the auklet colony at Sirius Point enables rat numbers to increase when auklets are present during the spring and summer (Major & Jones, 2005). In addition, rat predation and disturbance has been linked to extreme variation in auklet reproductive success and slow chick growth at Sirius Point (Major *et al.*, 2006). However, a quantification of rat diet at Sirius Point and unequivocal direct evidence linking rats to breeding failure at the auklet colony in 2001 and 2002 are lacking. We hypothesized that as generalist predators rats will change diet with location to whatever the most readily available and highest nutritional quality prey may be, as suggested by Drever & Harestad (1998). If energetically rich prey are in high abundance, then rat populations would be expected to grow rapidly and exhibit high reproductive success, as was the case at Sirius Point and Christine Lake in 2002 and 2003 (Major & Jones, 2005). Thus at these locations we expected that rats fed at a higher trophic level than those at East Kiska Lake and from a marine source of carbon. Furthermore, we expected that if rats are preying predominantly on least auklets at Sirius Point, then rat isotopic signatures would match those predicted by auklet isotopic signature.

Our results confirm the suspicion that at Sirius Point, rats prey on auklets. This may have severe implications for the auklet colony. Population viability analysis for auklets at Kiska indicates that the current population size cannot be

maintained and may experience a 92% reduction over 30 years if the current reproductive failure continues (Major, 2004). However, isolating rats as the sole and unequivocal cause of extremely low auklet reproductive success has proved to be challenging (Major *et al.*, 2006). Previous work inferred rat prey selection from the contents of hoards found early in the auklet breeding season and the presence of predated individuals and eggs on the colony. This work suggested that rats kill and hoard large numbers of adult least auklets early in the auklet breeding season and kill adults, subadults, nestlings and eggs throughout the auklet breeding season (Major & Jones, 2005). The results from the current study confirm that rats do depredate auklets at Sirius Point and suggests that they play an important role in the observed low auklet reproductive success.

General ecological implications

Our results revealed striking variability in rat diet across Kiska Island. From our multiple-source mixing model, we can infer the food webs at each of our three study locations. However, these models assume that predators consume all potential prey items and thus tend to overestimate the contributions of prey types rarely consumed and underestimate the contributions of prey types commonly used (Rosing, Ben-David & Barry, 1998). Even so, our model reveals that rats at East Kiska Lake prey predominantly on terrestrial vegetation, rats at Christine Lake prey upon a wide range of all potential prey items, and rats at Sirius Point prey on intertidal invertebrates and auklets.

Rats can maintain moderate to high population levels in the absence of seabirds and even in the absence of access to littoral sources of food. Thus even though a seabird colony (e.g. Sirius Point) may provide poor over-wintering habitat for rats (birds absent, sparse vegetation and limited access to beaches and other intertidal areas), other areas provide a source of rats that invade and depredate the seabird colony.

Furthermore, as seabird populations are *k*-selected, adult survival being crucial in maintaining the population, they are particularly vulnerable to adversity (Croxall & Rothery, 1991). As rats appear to feed on adults as well as chicks and eggs at Kiska (Major & Jones, 2005), a least auklet population crash may be inevitable. In general because rats can survive without seabirds as a source of food, if a seabird population crashes, rat numbers will likely continue to be high, making seabird recolonization impossible, as any recolonizing individuals would experience intense predation pressure. In light of this we recommend that all mitigation plans address not only eradicating/controlling rats at seabird colony sites but also keeping potential invaders from returning. It is clear from our results that understanding the ecology of these non-seabird colony rats is vitally important for the conservation of insular avifauna and the ecological restoration of islands.

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