



Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets

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We determined whether a marine diving bird, the rhinoceros auklet, *Cerorhinca monocerata*, used different foraging behaviour and collected different prey items for its young than when feeding itself. Foraging behaviour was determined by conducting visual scans, and prey items were sampled by collecting fish delivered to chicks and by collecting fish where auklets were self-feeding, which was verified by two other sources of information. Adult auklets ate small fish (59.1 ± 0.5 mm, $N=547$), including juvenile Pacific sand lance, *Ammodytes hexapterus*, and Pacific herring, *Clupea harengus*, but collected larger fish to feed their chicks (95.2 ± 1.3 mm, $N=321$), including primarily Pacific sand lance, Pacific herring, Pacific salmon species, *Oncorhynchus* spp., and surf smelt, *Hypomesus pretiosus*. In addition, auklets collected fish for themselves primarily by diving in mixed-species feeding flocks before 1600 hours, whereas they collected fish to feed their chicks by diving solitarily after 1600 hours. This suggests that auklets switched both foraging behaviour and prey selection when collecting fish for self-feeding, compared with when collecting fish for chick provisioning. Several avian studies have documented different diets of adults and chicks, but this is the first research to observe directly and document different foraging behaviour used in adult and chick provisioning. We emphasize the importance of distinguishing between self-feeding and chick provisioning in foraging and life history studies.

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Few studies on animals provisioning their young have distinguished between food that parents collect for themselves (self-feeding) and food they collect for their young (provisioning). Although this distinction has been recognized for some time (Hegner 1982; Kacelnik 1984; Swihart & Johnson 1986), it has been the focus of optimal modelling only in the last decade (Houston 1987; Kacelnik 1988; Kacelnik & Cuthill 1990; Ydenberg 1994; Ydenberg et al. 1994; Saunders & Ydenberg 1995). It is important to distinguish between self-feeding and provisioning because it is predicted that parents do not value equally the prey collected under these two foraging contexts (Ydenberg 1994; Ydenberg et al. 1994). When self-feeding, there are costs in collecting food but there are also energetic benefits from consuming the food. When provisioning, however, the benefits to the adult are in long-term fitness, rather than short-term energy balance. Therefore, with provisioning there are only the costs of collecting and delivering food, in the strict sense

of foraging theory. Adults having greater energetic costs than benefits while provisioning is consistent with a central concept in classical life history theory, which assumes that reproduction has a survival cost due to deficits acquired in the adult's short-term energy balance (Drent & Daan 1980; Partridge & Harvey 1985; Reznick 1985; Kacelnik 1988; Martins & Wright 1993). Therefore, distinguishing between self-feeding and provisioning not only broadens the scope of foraging theory, but also allows researchers to examine the long-term survival cost of reproduction by comparing the short-term adjustments in foraging decisions when self-feeding to those when provisioning (Kacelnik 1988; Ydenberg 1994).

Birds often collect different prey items for their chicks than for themselves. When transporting meals to chicks, larger or higher-quality (e.g. higher protein or lipid content) prey items are often collected for delivery to young compared with those ingested by parents (Cairns 1984; Bradstreet & Brown 1985; Robinson 1986; Swihart & Johnson 1986; Piatt 1987; Vermeer et al. 1987; Mahon et al. 1992). Most studies have only examined dietary differences between adults and their young, but have not reported preferences for foraging behaviour in each foraging context. Although selection of prey types and foraging methods are closely linked, observed differences

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in both parameters could indicate differences between provisioning and self-feeding behaviour.

We determined whether different foraging methods and different prey items were selected when self-feeding compared to when provisioning nestlings in a marine bird, the rhinoceros auklet, *Cerorhinca monocerata* (family Alcidae). This auklet dives underwater to feed mainly on small schooling fish (Vermeer et al. 1987; Gaston & Dechesne 1996). It forages both solitarily and socially in mixed-species feeding flocks (Sealy 1973; Hoffman et al. 1981; Porter & Sealy 1981, 1982; Grover & Olla 1983). It is a colonial breeder and lays a single-egg clutch (Gaston & Dechesne 1996). The chick-rearing phase lasts 40–50 days, during which time parents collect 1–30 intact fish in their bills and deliver these fish to their chicks at night (Gaston & Dechesne 1996). It is easy to distinguish between self-feeding and provisioning in auklets because adults hold fish in their bills for delivery to their chicks and provision the chick once a day.

METHODS

Study Area

We conducted this study on and near the Seabird Rocks breeding colony on the west coast of Vancouver Island, just south of Barkley Sound (48°45'N, 125°09'W). This small island (500 × 300 m) is situated on the exposed Pacific coast and supports approximately 130–170 breeding pairs of rhinoceros auklets (Rodway 1991). This colony is small compared with many other rhinoceros auklet colonies (e.g. Triangle Island: 41 680 breeding pairs; Rodway 1991) and is located less than 2 km from the coastline. The concentration of auklets around this colony and close to shore during the breeding season make this an ideal study area.

Observations of Foraging Behaviour

We observed rhinoceros auklets at sea during chick rearing in 1996 and 1997 using instantaneous visual scans from a fixed point on land (Martin & Bateson 1986). We conducted scans using a 15–45 × power zoom spotting scope from the same observation point each day, which was situated more than 5 km away from the breeding colony. The scanning area was frequently used by foraging auklets throughout the day during the breeding season and also was used as a staging area where auklets aggregated before flying to the colony at night. We conducted 1-h observation bouts, separated by at least 1 h. We divided each 1-h observation bout into three 20-min intervals, during which we scanned three distinct areas sequentially. We selected the first two scan areas at random, to ensure that scans were not conducted in the same order in each hour. We conducted an average of three 1-h observation bouts per day (range 1–6) during daylight.

Each 20-min scan consisted of watching one field of view in the spotting scope for 90 s, then moving the scope to the next field of view. We selected this observation period (90 s) to document all diving/

resurfacing bouts within a given period (dive duration: 45.0 ± 1.2 s, $N=75$, 10 birds observed; maximum dive duration: 69 s; Burger et al. 1993). In each field of view, we recorded the number of adult auklets engaged in foraging activities. The total foraging time (Foraging) included both solitary diving and flock diving. We also recorded the total number of auklets on the water, holding fish and associated with feeding flocks, and the number of feeding flocks. Auklets diving in a feeding flock, flying and swimming towards and away from a feeding flock, or resting and preening in a dissipated flock were considered to be associated with feeding flocks.

Between visual scans in 1996, we recorded dive and inter-dive recovery (pause) durations of solitary auklets. We measured dive and pause durations of auklets to the nearest second using a stopwatch and recorded all observations on a tape recorder. An individual was tracked until it terminated its dive bout, was lost from sight, or was confused with other conspecifics (focal animal technique; Martin & Bateson 1986). Termination of a dive bout was assumed if the bird began prolonged preening, surface flapping or bathing (two standard deviations above the mean pause duration). Pauses can be missed because rhinoceros auklets can travel long distances under water during a dive (50 m; Burger et al. 1993) and their bills may emerge only momentarily for breathing (L. Paul, personal communication). Therefore, dives exceeding two standard deviations above the mean were discarded. Dive and pause durations of auklets diving in mixed-species feeding flocks could not be recorded because it was impossible to follow one individual in a flock of many conspecifics.

Analysis of Observations

The number of auklets engaged in each foraging activity during each successive 20-min scan was averaged to obtain hourly means. These means were then used to calculate the mean percentage of auklets in the surveyed population engaged in each foraging activity in each hour. We calculated percentages by dividing the mean number of auklets engaged in each activity during an hour by the mean number of auklets observed on the water in that hour. These proportions were then arcsine square-root transformed to meet the underlying assumptions of normality (Zar 1984, page 239). We also averaged the total number of feeding flocks and the total number of auklets observed on the water, associated with feeding flocks and holding fish to obtain hourly means. We used two-way ANOVAs for unbalanced designs (SYSTAT 1992) to compare these hourly means and to compare the transformed proportions between years and between two time categories: morning and afternoon (before 1600 hours) and late afternoon and evening (1600 hours and after). We used a one-way ANOVA for unbalanced designs (SYSTAT 1992) to compare the mean number of auklets holding fish and the transformed proportions of auklets diving solitarily and Foraging after 1600 hours among three phases (incubation, chick rearing and postfledging) in the 1996 breeding season.

Sampling and Analysis of Diets

We collected the fish delivered as meals to chicks during chick rearing from 1995 to 1997 in two ways. First, we blocked the entrances of burrows to prevent fish-carrying parents from entering (Hatch 1984), causing parents to drop their fish near the burrow entrance. We used screens of galvanized hardware cloth (1.25-cm mesh) sized appropriately for auklet burrows (ca. 18×18 cm) to block entrances. Approximately 35–40 burrows were screened 1 h before auklets began returning to the colony at dusk (ca. 2000 hours) and the same burrows were screened throughout the study for a maximum of four nights per 40–50-day chick-rearing period. Screens were left in burrow entrances for the entire night and were checked every 30 min during the peak arrival time of auklets (2200–0200 hours). During these checks, we searched the screens and surrounding areas for fish. We placed any fish we found in a labelled bag, keeping samples collected from each screen separate. We then washed the fish with salt water to remove dirt, identified them to species, weighed them, and measured the standard length (snout to caudal peduncle) of each.

Second, we collected fish delivered to chicks by capturing auklets returning to the colony at night with food in their bills. We captured auklets by hand near a bare strip of land that was used as a landing spot ('runway') by auklets when returning to the colony. We placed samples from individual adults in separate labelled bags. We then cleaned the fish and measured them, as described above.

We collected samples of fish from schools beneath flocks of feeding birds throughout daylight (0700–1900 hours) during chick rearing in 1995 and 1996. We collected fish by driving a small boat through a flock of foraging birds and dipnetting the fish that were at a depth of less than 0.5 m. The net opening was circular with a 0.5-m diameter and a mesh size of 2 cm. We later identified fish to species, weighed them and measured the standard length of each. When auklets surfaced with fish in their bills at feeding flocks, we visually estimated fish size by comparing the length of the fish to the length of the auklet's bill (culmen: 33.3 ± 1.3 mm, $N=39$; Gaston & Dechesne 1996). This confirmed that the fish sizes we sampled were similar to those collected by auklets. We used two-way ANOVAs for unbalanced designs to compare the standard lengths of fish collected between years and between the two location categories: the colony and mixed-species feeding flocks.

RESULTS

Foraging Behaviour

During chick rearing in 1996 and 1997, the percentage of auklets observed Foraging increased throughout the day and peaked in the late afternoon and evening (after 1600 hours), due to an increase in the percentage of auklets diving solitary in the evening (Figs 1, 2, Table 1). The number of auklets holding fish, presumably for delivery to chicks, increased significantly after 1600

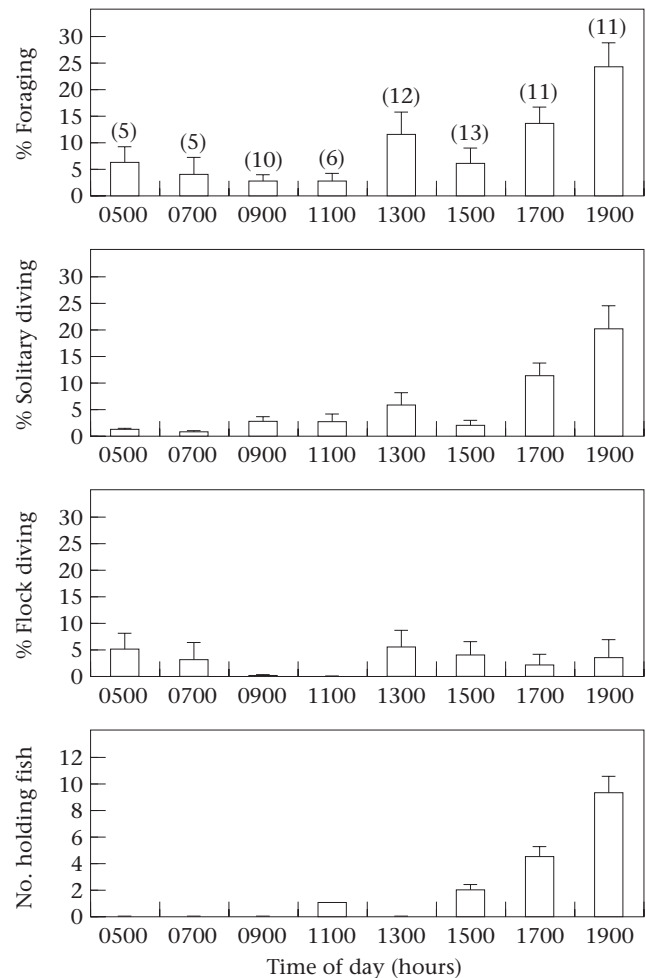


Figure 1. The mean + SE percentages of rhinoceros auklets engaged in foraging activities/2 h and the mean + SE number of auklets holding fish/2 h during chick rearing in 1996. The numbers in parentheses indicate the number of hourly scans/time interval.

hours, which coincided with the increase in the percentage of auklets diving solitary (Figs 1, 2, Table 1).

During daylight, rhinoceros auklets frequently joined feeding flocks, often mixed-species feeding flocks of gulls, common murres, *Uria aalge*, and cormorants. The percentage of auklets diving in feeding flocks did not vary significantly with time of day between 0500–2000 hours (Figs 1, 2, Table 1). After 1600 hours, there was a decrease in the number of auklets on the water and associated with feeding flocks, but there was no significant change in the number of feeding flocks being formed (Figs 3, 4, Table 1). Therefore, feeding flocks still formed after 1600 hours, but auklets within these flocks did not appear to forage to the same extent as earlier in the day.

In 1996, when observations spanned the entire breeding season (24 May–3 September), the percentage of auklets holding fish after 1600 hours differed significantly between chick rearing ($21.7 \pm 5.0\%$, $N=33$), incubation ($5.6 \pm 5.6\%$, $N=6$) and postfledging ($0.2 \pm 0.2\%$, $N=7$; one-way ANOVA on arcsine square-root transformed proportions: $F_{2,44}=6.1$, $P=0.005$). In addition, the

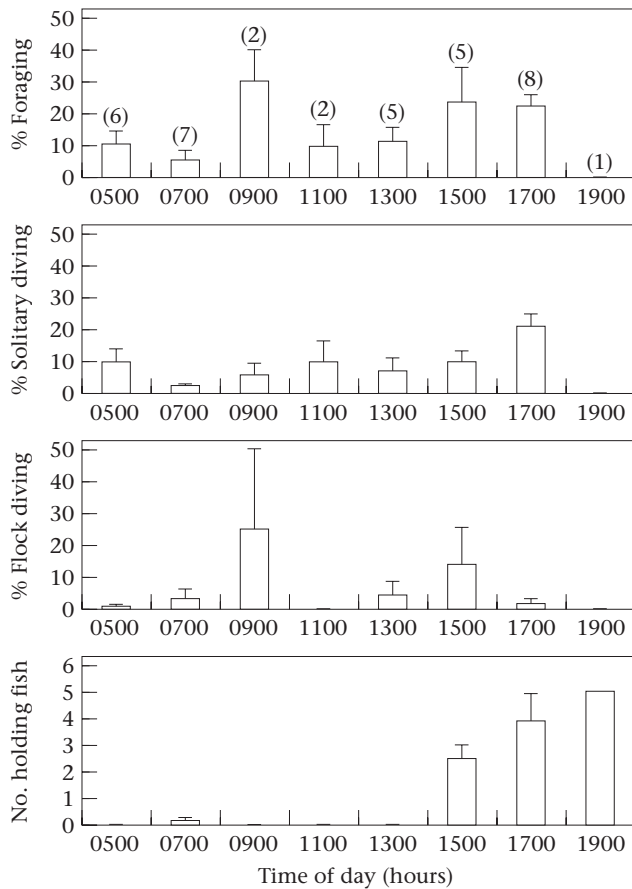


Figure 2. The mean+SE percentages of rhinoceros auklets engaged in foraging activities/2 h and the mean (+SE) number of auklets holding fish/2 h during chick rearing in 1997. The numbers in parentheses indicate the number of hourly scans/time interval.

percentage of auklets diving solitarily after 1600 hours differed significantly between chick rearing ($11.5 \pm 2.2\%$), incubation ($5.6 \pm 1.9\%$) and postfledging ($3.6 \pm 1.2\%$), $F_{2,44}=4.2$, $P=0.022$). Foraging before 1600 hours, however, did not differ between chick rearing ($14.2 \pm 2.4\%$), incubation ($9.7 \pm 1.3\%$), and postfledging ($8.5 \pm 0.3\%$;

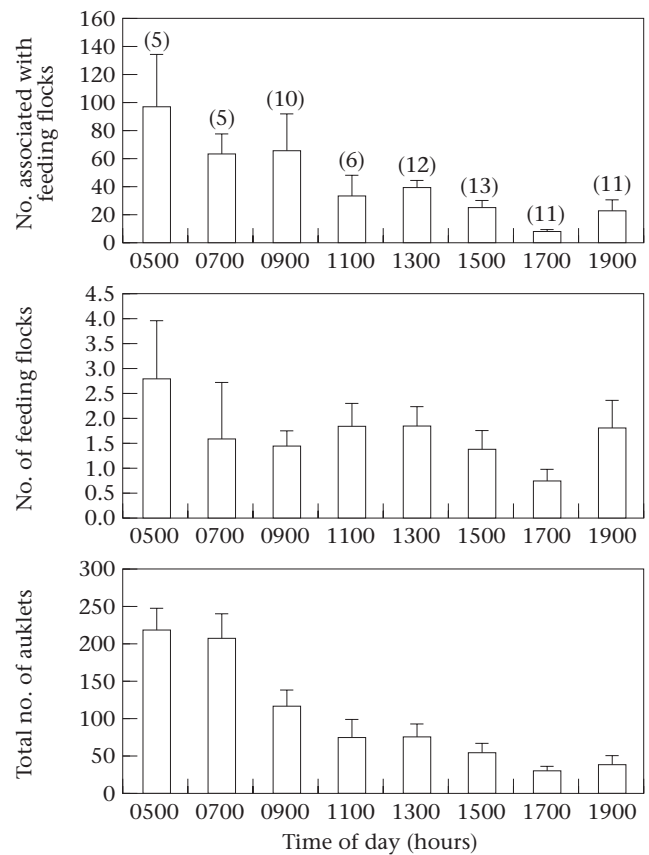


Figure 3. The mean+SE number of rhinoceros auklets associated with feeding flocks, the mean number of feeding flocks, and the mean number of auklets on the water/2 h during chick rearing in 1996. The numbers in parentheses indicate the number of hourly scans/time interval.

$F_{2,44}=0.1$, $P=0.908$). Prey availability also did not increase in the evening, and the composition of fish in surface waters did not change with time of day (Davoren 1997). Thus, the increase in solitary diving after 1600 hours during chick rearing was primarily due to the increased foraging by parents collecting fish for their chicks.

Table 1. The mean±SE activity percentages, number of rhinoceros auklets and number of feeding flocks before and after 1600 hours in 1996 and 1997

Activity or number	1996		1997		<i>F</i> statistic*			<i>P</i>	
	Before 1600	After 1600	Before 1600	After 1600	Time	Year	<i>df</i>	Time	Year
Foraging (% of scanned auklets)	6.9±1.6	14.2±2.4	9.7±1.9	21.1±4.2	17.4	10.6	1,98	<0.0001	0.002
Solitary diving (%)	3.7±0.8	11.5±2.2	7.5±1.6	15.7±3.3	22.6	12.8	1,98	<0.0001	0.001
Flock diving (%)	3.2±1.3	2.7±1.4	2.2±1.4	5.4±3.7	0.5	0.1	1,98	0.495	0.759
No. of auklets holding fish	0.1	4.4±0.1	0.1	3.5±0.7	6.6	1.1	1,51	0.013	0.304
No. of auklets associated with feeding flocks	31.8±7.3	8.7±2.9	12.6±7.2	3.4±2.0	6.7	10.2	1,68	0.012	0.002
No. of feeding flocks	1.9±0.3	1.2±0.2	0.5±0.2	0.4±0.2	1.5	12.9	1,98	0.230	0.001
No. of auklets on the water/scan	117.3±12.9	39.7±6.7	76.7±12.8	24.6±3.7	21.6	3.3	1,98	<0.0001	0.072
No. of hourly scans	40	33	22	13					

*Comparisons between the two time of day categories and the 2 years were performed using a two-way ANOVA for unbalanced design. There was insufficient evidence ($P>0.05$) for an interaction between time and year. For the activity percentages, these tests were performed on the arcsine and square-root transformed proportions.

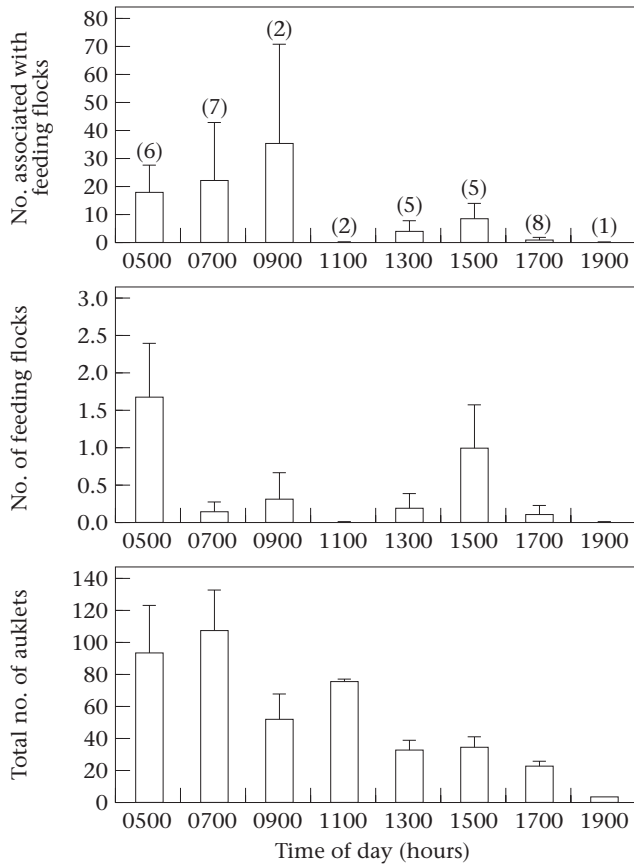


Figure 4. The mean±SE number of rhinoceros auklets associated with feeding flocks, the mean number of feeding flocks, and the mean number of auklets on the water/2 h during chick rearing in 1997. The numbers in parentheses indicate the number of hourly scans/time interval.

All of these trends were similar in 1996 and 1997 (Figs 1–4, Table 1), but there were some differences between years. In 1997, there were significantly fewer feeding flocks and fewer auklets associated with feeding flocks compared with 1996 (Table 1). In addition, the

percentage of auklets observed Foraging was significantly higher in 1997 compared with 1996, due to an increase in the percentage of auklets diving solitarily (Table 1). The total number of auklets on the water did not differ significantly between years (Table 1).

When diving solitarily, the mean ± SE dive duration was 37.6 ± 0.8 s (855 dives made by 139 birds) and the mean ± SE pause duration was 10.7 ± 0.7 s (845 pauses made by 139 birds). Two per cent of the dive durations recorded were discarded because they exceeded two standard deviations above the mean. Unquantified observations of auklets foraging in mixed-species feeding flocks suggest that dive durations by auklets ranged between 10 and 15 s, and pause durations ranged between 1 and 3 s.

Diet

In all 3 years, 90–99% of the prey items delivered to chicks comprised four species of fish: Pacific sand lance, *Ammodytes hexapterus*, salmon species *Oncorhynchus* spp. Pacific herring, *Clupea harengus*, and surf smelt, *Hypomesus pretiosus*, except in 1997 when surf smelt was not delivered to chicks (Table 2). In contrast, in 1995 and 1996, only two fish species (Pacific herring and Pacific sand lance; Table 2) were collected from surface waters where mixed-species feeding flocks had been foraging.

Auklets captured larger fish to feed their chicks than to feed themselves. Two age classes of sand lance (Vermeer & Westrheim 1984) were delivered to chicks: 0+ class (juveniles, 40–110 mm) and 1+ class (111–180 mm). Similarly, chicks received 0+ (juveniles, 40–100 mm) and 1+ (101–140 mm) age classes of herring (Hart 1973). The salmon and surf smelt delivered to chicks were all juveniles (smolts) and adults, respectively. Sand lance and herring collected from surface waters beneath feeding flocks were all juveniles (0+). Fish observed in the bills of auklets from mixed-species feeding flocks were one to two times the length of the auklet’s bill (herring: 47.7 ± 0.3 mm, N=26; sand lance: 70.1 ± 0.3 mm, N=21), which corresponded to the size of fish captured in the

Table 2. Mean±SE standard lengths in mm of each fish species delivered to rhinoceros auklet chicks at the Seabird Rocks colony in 1995, 1996 and 1997, and collected with a dipnet at mixed-species feeding flocks containing rhinoceros auklets in 1995 and 1996

Location, year	Sand lance	Herring	Salmon	Surf smelt	Other species*
Colony, 1995	87.5±1.9 (128)†	86.7±7.0 (15)	87.8±3.8 (18)	134.2±4.5 (16)	87.8±12.5 (4)
Colony, 1996	107.2±1.9 (65)	82.5±8.3 (14)	97.8±1.8 (30)	113.8±14.0 (8)	71.0±6.8 (5)
Colony, 1997	79.9±3.4 (37)	144.8±6.7 (6)	98.8±2.2 (25)	0	46.9±2.1 (8)
Feeding flock, 1995	74.1±0.6 (42)	51.4±1.0 (138)	0	0	0
Feeding flock, 1996	68.0±0.5 (163)	53.9±0.5 (204)	0	0	0

*Other species found include: Pacific sandfish, *Trichodon trichodon* (N=6), Pacific hake, *Merluccius productus* (N=4), and rockfish *Sebastes* spp. (N=7).

†Numbers of fish collected are given in parentheses.

dipnet (Table 2). Larger fish, requiring more manipulation, would be more likely to be brought to the surface than smaller ones, but they were not observed in our scans or focal observations. Juvenile herring and sand lance also were the primary diets of adult rhinoceros auklets collected in salmon gill nets in the late summer near the study area from 1993 to 1996 (M. L. Wilson 1998). Overall, the sand lance sampled at feeding flocks, both visually and via dipnet, were significantly smaller than those delivered to chicks in both years (two-way ANOVA: $F_{1,415}=314.3$, $P<0.0001$; Fig. 5). Similarly, the herring sampled at feeding flocks were significantly smaller than those delivered to chicks in both years ($F_{1,393}=163.2$, $P<0.0001$; Fig. 5). With all species combined, the fish sampled at feeding flocks were significantly smaller than those delivered to chicks in both years ($F_{1,911}=952.1$, $P<0.0001$; Fig. 6). Although fish at feeding flocks were not collected in 1997, when fewer flocks were observed, the fish that were delivered to chicks again consisted of both 1+ and juvenile sand lance and only 1+ herring (Fig. 5).

DISCUSSION

Self-feeding versus Provisioning: Prey Types

Results revealed significant differences between the prey delivered to chicks and those available in surface waters at feeding flocks, where adult rhinoceros auklets primarily fed themselves. Chick meals included a substantial portion of larger fish, such as large adult (1+) sand lance and herring, salmon smolts and adult smelts, whereas the fish at feeding flocks were all small juvenile (0+) herring and sand lance. The species composition of chick meals in our sample was similar to that found at the same colony in 1986–1989 (Burger et al. 1993) and elsewhere in North America (Vermeer 1980; Hatch 1984; Vermeer & Westrheim 1984; Vermeer & Devito 1986; Wilson & Manuwal 1986; Bertram et al. 1991; Bertram & Kaiser 1993). The majority of chick meals (81%) comprised one or two large fish, sometimes accompanied by a few smaller fish. Fewer meals (19%) comprised 10 or more small fish such as juvenile sand lance, herring or rock fish, *Sebastes* spp.

Although chick diets are well studied, those of adult rhinoceros auklets are not (Vermeer et al. 1987). Adult diets can include large proportions of crustaceans (Kozlova 1957) and juvenile fish (Sanger 1987), which would be unsuitable for chick meals due to their small sizes. In general, alcids that deliver intact prey in their beaks to chicks tend to select much larger prey for chick meals than the adults ingest themselves (Bradstreet & Brown 1985; Vermeer et al. 1987; Baird 1991). This dichotomy in prey selection between self-feeding and provisioning fits the central place foraging model, in which efficient adults should select larger loads and larger prey types for delivery to the nest site (Orians & Pearson 1979; Hegner 1982; Cuthill & Kacelnik 1990; Kaspari 1991; Sodhi 1992; Wanless et al. 1993; Burness et al. 1994; Frey et al. 1995).

The small juvenile herring and sand lance available at the feeding flocks in our study represent suboptimal chick meals, both in terms of potential load mass and food quality. Even with an unlimited supply of these small fish, parents may not have been able to maximize food loads delivered to chicks. Thirty fish is the maximum number of fish known to be delivered to chicks of rhinoceros auklets (Gaston & Dechesne 1996). The fish found at feeding flocks were 0.7 ± 0.3 g ($N=547$) and, therefore, the maximum loads of such fish a parent could deliver would usually range between 12 and 30 g (30 fish with a minimum size of 0.4 g and a maximum size of 1.0 g). In contrast, food loads containing only large fish in this study (i.e. surf smelt and adult herring), were 49.7 ± 3.7 g ($N=22$). Other studies of rhinoceros auklets showed that larger meals contained larger than average fish (Vermeer & Devito 1986; Bertram et al. 1991; Burger et al. 1993), which is generally true for multiple prey loaders (Montevecchi 1993). This suggests that parents maximized the mass of fish delivered to chicks by selecting larger prey items. In addition, selecting a few large fish may reduce the difficulties of manipulating many prey items in the bill at the same time (the 'loading effect'; Pyke 1984).

Juveniles also had lower caloric densities than larger fish. Using samples of sand lance and herring taken from rhinoceros auklets, Vermeer & Devito (1986) found that 0+ juveniles ($\bar{X}=80$ mm long, 19.68 kJ/g for sand lance; $\bar{X}=72$ mm, 19.94 kJ/g for herring) had lower energy contents than the 1+ cohorts ($\bar{X}=155$ mm, 22.54 kJ/g for sand lance; $\bar{X}=175$ mm, 25.34 kJ/g for herring). These represented energy increases of 15 and 27%, respectively. Overall, meals comprised of juvenile fish, such as those available at feeding flocks, provided the lowest caloric values (Vermeer & Devito 1986).

Self-feeding versus Provisioning: Timing of Foraging

Rhinoceros auklets foraged for themselves throughout the day, but collected meals for their chicks only in the last third of the daylight. Nocturnal delivery of chick meals is thought to reduce the risks of predation (by falcons and eagles) and kleptoparasitism (by large gulls) at the breeding colonies (Paine et al. 1990; Watanuki 1990; Harfenist & Ydenberg 1995). These risks also explain why parents typically make only one trip to the colony each night to deliver fish to their chicks and why auklets sometimes avoid the colony on clear, moonlit nights (Leschner 1976; Wilson 1977).

Rhinoceros auklets do not act as 'classical' central place provisioners, because they deliver food to their chicks typically once each day. Most animals in which central place foraging models have been tested commute between feeding and nesting or food cache sites numerous times per day (Orians & Pearson 1979; Pyke 1984). Efficient central place foragers tend to increase the load size or prey size (in single-prey loaders) with increasing distance from the nest or food cache site (Orians & Pearson 1979; Hegner 1982; Cuthill & Kacelnik 1990; Fryxell & Doucet 1991; Kaspari 1991; Sodhi 1992;

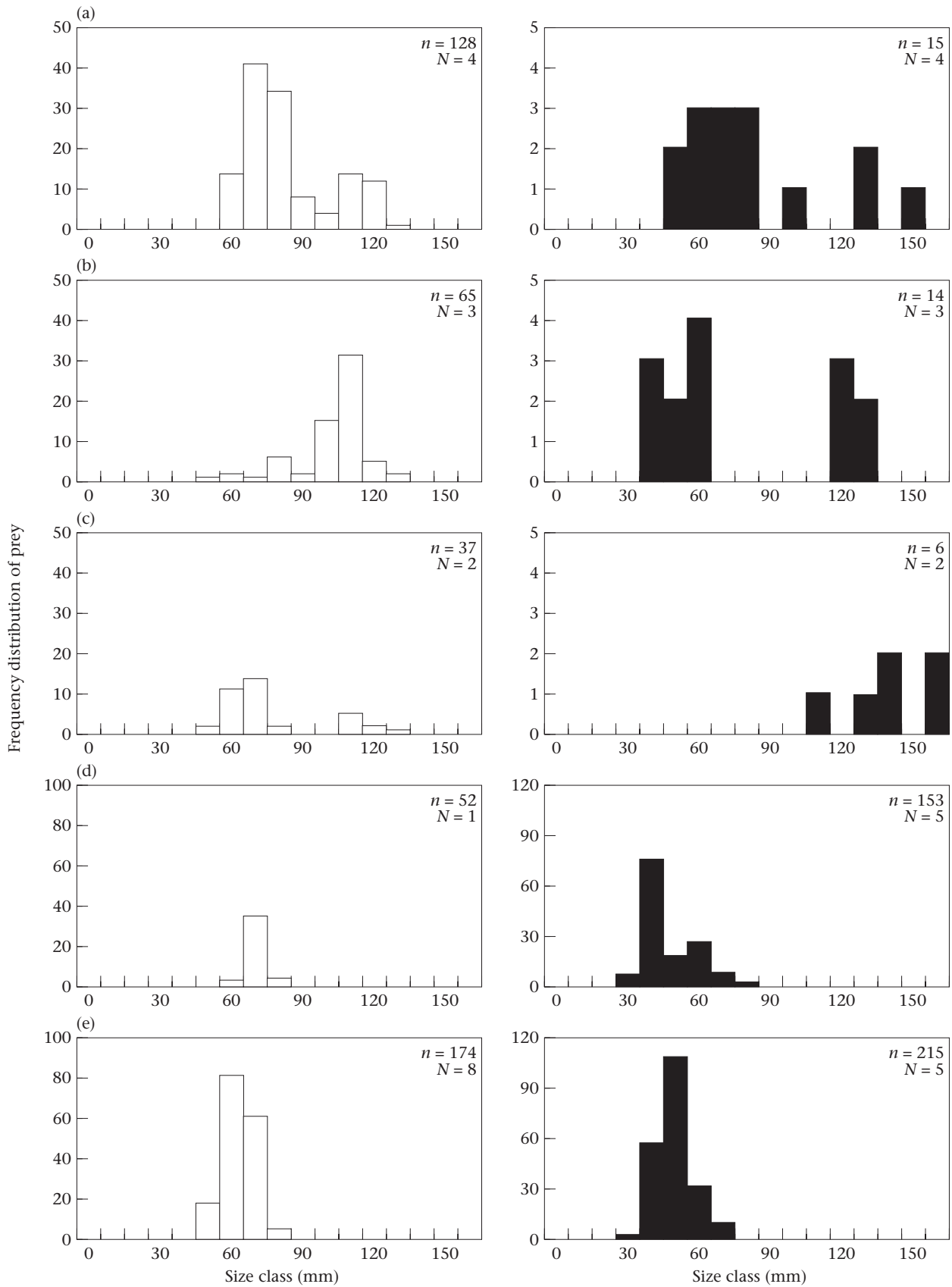


Figure 5. The frequency distribution of size classes of sand lance (□) and herring (■) collected from adult rhinoceros auklets provisioning chicks at the colony in (a) 1995, (b) 1996 and (c) 1997, and collected via dipnet (or estimated via visual observation) at feeding areas containing auklets in (d) 1995 and (e) 1996. N indicates the number of sample periods (nights or days, respectively) that fish were collected at the colony and at flock feeding areas, and n represents the number of fish collected.

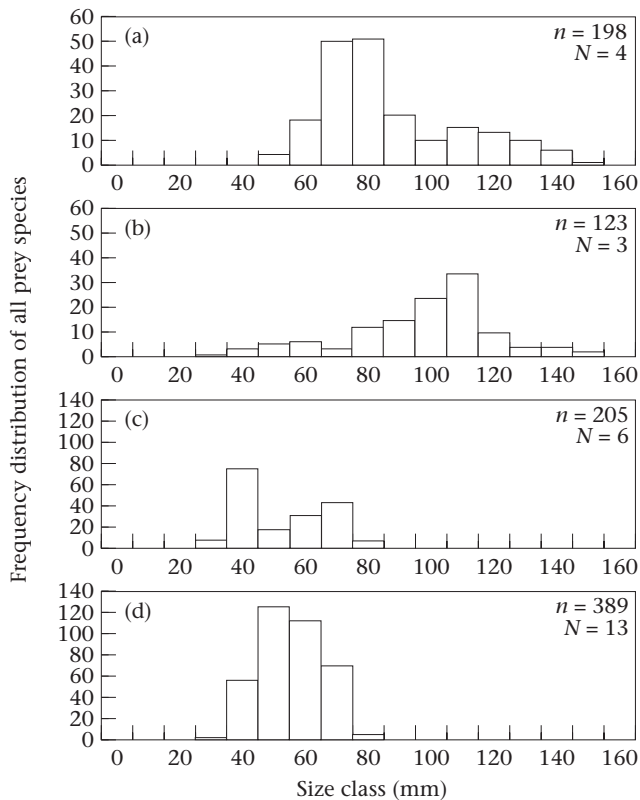


Figure 6. The frequency distribution of size classes of all fish species collected from adult rhinoceros auklets provisioning chicks at the colony in (a) 1995 and (b) 1996, and collected via dipnet (or estimated via usual observation) at feeding areas containing auklets in (c) 1995 and (d) 1996. N indicates the number of sample periods (nights or days, respectively) that fish were collected at the colony and at flock feeding areas, and n represents the number of fish collected.

Bowers & Ellis 1993; Wanless et al. 1993; Burness et al. 1994; Giraldeau et al. 1994; Frey et al. 1995). This maximizes food delivery per unit of energy expended during each trip (Waite & Ydenberg 1996). With only a single provisioning of chicks each day, auklets should always maximize food loads, regardless of the distance travelled. This in turn affects the diurnal variations in their foraging decisions and separates the periods of self-feeding and provisioning. Collection of chick meals occurred only towards the end of the day, as indicated by the increasing number of auklets holding fish in their bills after 1600 hours. Capture and holding of fish for chick meals earlier in the day would probably inhibit the auklets own self-feeding (capturing and ingesting prey may be difficult with a large fish held in the beak) and reduce the quality of the chick meal. In particular, a fish held for several hours is likely to dehydrate (Montevecchi & Piatt 1987) and fish appear to be the only source of water for nestlings.

Self-feeding versus Provisioning: Behavioural Differences

Self-feeding rhinoceros auklets used a mixed strategy, of solitary and flock foraging. They are commonly found

in mixed-species feeding flocks (Sealy 1973; Hoffman et al. 1981; Porter & Sealy 1981, 1982) and thereby gain the benefits of social foraging (Wittenberger & Hunt 1985; Gotmark et al. 1986; Valone 1989). In particular, flock foraging, which centres on schools of juvenile fish near the surface, facilitates the location of prey, allows shallow dives and provides access to large numbers of readily caught prey (Hoffman et al. 1981). Kleptoparasitism was not a problem because the auklets primarily swallowed their prey underwater (Sealy 1973; Grover & Olla 1983), and short-term prey depletion seemed unlikely because the fish schools generally dived deeper or dispersed before being depleted (personal observation). Flock foraging was not always an option, however, and in 1997 fewer flocks were recorded than in 1996. This decrease in the number of feeding flocks appears to be related to prey and birds being less concentrated in 1997, rather than due to a decrease in prey abundance (Davoren, *in press*).

In contrast, foraging for chick meals primarily involved solitary foraging and more-prolonged dive durations. This was shown by the increase in solitary foraging and auklets holding fish towards the end of the day, and by the significantly higher percentage of auklets diving solitary after 1600 hours during chick rearing, compared with incubation and postfledging in the 1996 breeding season. There were at least two reasons why adults switched to solitary foraging when provisioning. First, the fish available at the feeding flocks were small juveniles, which would limit the size of chick meals. Capturing larger fish evidently requires deeper dives for less obvious prey. Second, rhinoceros auklets and other alcids rarely surface with fish in their bills while foraging in mixed-species feeding flocks (Sealy 1973; Grover & Olla 1983; Mahon et al. 1992) and those that do are usually subject to kleptoparasitic attacks by gulls (Hoffman et al. 1981). Common murrelets holding fish in their bills tend to surface further from the centre of the flocks (Hoffman et al. 1981). Other studies also suggest that rhinoceros auklets (Sealy 1973) and marbled murrelets, *Brachyramphus marmoratus* (Mahon et al. 1992), avoid feeding flocks when collecting chick meals. Thus, solitary diving may reduce the risk of kleptoparasitism.

Optimality of Provisioning Behaviour

Foraging studies have only recently investigated the distinction between self-feeding and provisioning of offspring (Ydenberg 1994; Ydenberg et al. 1994). Differences in prey types used for self-feeding and provisioning have been documented several times in seabirds (e.g. Bradstreet & Brown 1985; Vermeer et al. 1987), and the reasons for selecting larger prey for nestlings are consistent with models of central place foraging (see above). Ours is the first study to show that these differences can be accompanied by switches in foraging behaviour. Provisioning rhinoceros auklets switched from a mixed strategy of solitary and flock foraging to primarily solitary foraging, and from exploiting small, juvenile fish captured near the surface to larger, sometimes mature fish captured with prolonged dives. The nocturnal visits of

auklets to the colony also determined that self-feeding and provisioning behaviour occurred sequentially. This makes an interesting deviation from the provisioning behaviour found in most animals and used in provisioning models (Ydenberg 1994; Ydenberg et al. 1994). Typically, self-feeding is interspersed with provisioning through the time available for foraging, and the allocation of time and energy to provisioning depends on the gains and costs of self-feeding (Ydenberg et al. 1994). Efficient self-feeding is a requisite of efficient provisioning. Further quantification of the energetic costs and benefits of these behaviours might be possible through intensive observations of individuals using radio-telemetry and doubly labelled water (Kooymann et al. 1992; Montevecchi et al. 1992; Chappell et al. 1993; Mehlum et al. 1993; Monaghan et al. 1994; Irons 1998), coupled with caloric measures of all prey types.

In the case of rhinoceros auklets, the sequential separation of self-feeding and provisioning does not reduce the benefits of efficient self-feeding. An adult that had not met its required daily food intake as evening approached would be less likely to have sufficient time to locate and capture the less obvious, larger fish, which make large chick meals. Behaviour that facilitates self-feeding, such as socially facilitated flock foraging at near-surface schools, would allow effective self-feeding, and hence allow adequate time for seeking alternative prey for chick meals later in the day.

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