MALE-FEMALE DIFFERENCES IN PARENTAL CARE IN MONOGAMOUS CRESTED AUKLETS

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Abstract. We studied patterns of parental care in Crested Auklets (*Aethia cristatella*), a monogamous seabird, for three breeding seasons (1996–1998) in the Aleutian Islands, Alaska, using radio-telemetry. In 1996, we found no sexual differences in parental care, low breeding site attendance rates, and reduced occurrences of copepods in food samples delivered to chicks, suggesting that food availability may have been low. In 1997 and 1998, we found significant differences in parental care between males and females, particularly early in the chick-rearing period: males attended and brooded their single chick 75% and 90% longer than females, while females provisioned 33% and 36% more often than males, respectively. We also found significant differences between prey types delivered to chicks by males and females for these two years. Males brought in 30% more euphausiids, a relatively large pelagic crustacean, than females, whereas females brought in 36% more copepods, a smaller crustacean, than males; however, prey mass per load did not differ. In 1998, we experimentally measured how vulnerable unattended young chicks were using models placed in unoccupied crevices. Eighty-three percent of the models showed signs of attack, presumably by conspecific adults. We concluded that unattended Crested Auklet chicks are highly vulnerable to attack. We suggest that males took on a greater role in chick brooding than their mates because they have a larger and more strongly hooked bill and are more aggressive than females, and thus better equipped than females to guard young chicks or the crevice breeding site.

Key words: Aethia cristatella, Crested Auklet, euphausiids, parental care, planktivore, seabird.

Diferencias en el Cuidado Parental entre Machos y Hembras en la Especie Monógama *Aethia cristatella*

Resumen. Utilizando radiotelemetría para estudiar los patrones de cuidado parental en *Aethia cristatella*, un ave marina monógama, durante tres períodos reproductivos (1996–1998) en las Islas Aleutianas, Alaska. En 1996 no encontramos diferencias sexuales en el cuidado parental, encontramos bajas tasas de presencia en el lugar de nidificación, y baja ocurrencia de copépodos en las muestras de alimento entregadas a los polluelos, lo cual sugiere que la disponibilidad de alimento podría haber sido baja. En 1997 y 1998 encontramos diferencias significativas en el cuidado parental entre hembras y machos, particularmente en el período temprano de cría de los polluelos. Los machos asistieron y empollaron su único polluelo por un período un 75% y 90% más largo que las hembras, mientras que las hembras aprovisionaron con una frecuencia un 33% y 36% mayor que los machos, respectivamente. También encontramos diferencias significativas entre el tipo de presa entregado por las hembras y por los machos durante los dos años. Los machos entregaron un 30% más de eufáusidos (crustáceos pelágico relativamente grandes) que las hembras, mientras que éstas entregaron un 36% más de copépodos (crustáceos más pequeños) que los machos. Sin embargo, el peso de la carga de alimento no varió. En 1998 medimos experimentalmente la vulnerabilidad de los polluelos no cuidados utilizando modelos situados en grietas desocupadas. El 83% de los modelos presentaron signos de ataques presumiblemente producidos por adultos coespecíficos. Concluimos que los polluelos no cuidados de *A. cristatella* son altamente vulnerables a ataques. Sugerimos que los machos tomaron un rol más importante en la crianza de los polluelos que sus parejas debido a que ellos presentan un pico más grande

y fuertemente arqueado y son más agresivos que las hembras. Por lo tanto están mejor equipados que las hembras para proteger a los polluelos o proteger el sitio de nidificación.

INTRODUCTION

Biparental care is prevalent among seabirds, which often rear young on isolated islands that offer protection from predators, but are far from food resources. The harsh environment in which high-latitude seabirds live means that substantial parental investment is required to raise offspring (Ashmole and Ashmole 1967, Lack 1968). Therefore, it is of interest to understand how seabird pairs coordinate the rearing of young in an environment with patchy and unpredictable prey (Lack 1968). Two important issues are (1) do socially monogamous males and females adopt similar parental roles? and (2) how are patterns of male-female parental care related to ecological factors such as food availability? Previous seabird studies have reported that males and females usually differ in their roles in rearing offspring (Burger 1981, Montevecchi and Porter 1980, Creelman and Storey 1991, Gaston and Jones 1998), an indication that males and females face different selection pressures.

How and why individuals vary in the level of their care of young may relate to a combination of factors. The amount of care provided by males may be determined by their confidence of paternity (Davies et al. 1992). In some cases males and females invest differently because of intersexual differences in size or aggressiveness that affect their effectiveness at the role of guarding offspring (Burger 1981). Variation among individuals may also occur due to ecological constraints, such as food availability (Uttley 1992). Individuals may also invest according to their mate's breeding status or quality (the "differential allocation hypothesis," Burley 1986). Furthermore, individuals may vary simply because of their ability or experience in rearing offspring (Gowaty 1996).

In this paper, we investigate patterns of parental care by males and females during the chick-rearing period in a crevice-nesting seabird, the Crested Auklet (*Aethia cristatella*, Jones 1993b). Crested Auklets are socially monogamous with low rates of extra-pair copulations (Hunter and Jones 1999), and the efforts of both parents are required to successfully rear their single, annual offspring (Fraser et al. 1999).

Both sexes incubate (approximately 35 days total) and care for the chick in a rock crevice until it departs the colony at about 35 days after hatching (Piatt et al. 1990, Fraser et al. 1999). This species is unusual among auks for the distinct sexual dimorphism in bill shape and size: males have a longer culmen and deeper bill than females and a strong hook at the bill tip (Jones 1993a). This bill dimorphism may be related to male intrasexual aggression (Jones and Hunter 1999), but may also have ecological consequences for foraging preferences or abilities (Bédard 1969a, Shine 1989). The focus of our study was to elucidate the roles of male and female Crested Auklets in parental care. Our specific objectives were to (1) quantify the parental roles (provisioning and brooding of the chick) of male and female Crested Auklets, (2) investigate whether brooding and provisioning are related to chick growth, and (3) determine whether males and females differ in the types of prey they feed to their chicks.

METHODS

STUDY AREA

We studied Crested Auklets on Buldir Island (52°21′N, 175°56′E) in the Aleutian Islands, Alaska, for three breeding seasons (1996–1998). Buldir is located in the western part of the island chain and provides habitat for one of the largest and most diverse seabird concentrations in the northern hemisphere (Sowls et al. 1978, Byrd and Day 1986). Our study area on Buldir was located at "Main Talus," a colony with an estimated 250 000 breeding Crested Auklets (Byrd et al. 1983).

DATA COLLECTION

MALE AND FEMALE PROVISIONING AND BREEDING SITE ATTENDANCE

Crested Auklets nest in rock crevices; therefore, quantification of parental care was difficult and visual observations of birds at breeding sites were not possible in most cases. We used radio-telemetry to acquire data on attendance at breeding sites. Transmitters (made by Biotrack; Dorset, UK, and Holohil, Carp, Ontario, Canada) were attached to metal leg bands. These transmitters had pulse rates of 38 to 80 beats min^{-1}

and each weighed 3.0 g (1% of adult mass). We placed short-range (<5 m) whip antennas at crevices, each connected to a Lotek (SRX 400; Newmarket, Ontario, Canada) receiver on coaxial cables 25 to 60 m in length. The receiver switched from one antenna to another, through the series, at 3–5 min intervals (depending on the number of antennas that were running, transmitter pulse rates, and number of frequencies being scanned). These records were stored on a data-logger and downloaded every 48 hr, weather permitting. This system (powered by a set of solar panels and a battery) allowed us to continuously monitor individuals' activities at or near their nesting crevices during the chick-rearing period. Visual observations of transmitter-tagged birds entering and leaving crevices confirmed that antennas were picking up signals only when individuals were in their crevice or within 3 m of it.

We followed pairs through incubation and began checking crevices daily near the expected hatch date. Both pair members were captured after their chick hatched, sexed by bill shape (Jones 1993a), measured, and tagged with individually identifiable radio-transmitters and colored plastic leg bands ($n = 7, 8, 6$ pairs, in 1996, 1997, and 1998). Each record for an individual on the data-logger was classified as either chick provisioning, chick brooding, or both. When an individual was logged at its crevice after an absence of more than 2 hr we assumed it had brought food. This assumption was based on 10–12 hr of continuous observations at our study plot: marked birds that returned within 2 hr rarely brought food with them, while those that returned after 2 hr invariably carried food. Brooding was assumed when telemetry indicated that the adult was with the chick during at least two consecutive scans (6–10 min). In any one bout, a bird could be assigned as both chick feeding and chick brooding. Each member of a pair was assigned a behavior regardless of its partner's behavior (e.g., if the pair spent the night in the crevice together, both were scored as brooding).

We quantified provisioning (chick feeding day^{-1} adult^{-1}) and breeding site attendance rates (min day^{-1} adult^{-1}) for males and females. All parental activities were quantified in relation to chick age, and average rates of individuals were used in the analysis. For the telemetry data, we divided the chick-rearing period up into two stages: chicks aged 2 to 14 days and chicks aged 15 to 25 days (hereafter referred to as early and late chick rearing) for three reasons: (1) coordination of parental activities was more critical in early chick rearing because of chick thermal requirements for brooding, (2) sexual differences in parental care activities were greater in early chick rearing, and (3) there was variability in transmitter life (mean ± SD 1996: 13.9 ± 3.8 days, $n = 14$; 1997: 27.7 ± 3.8 days, $n = 16$; 1998: 20.9 ± 7.7 days, $n = 12$). Male and female parental behaviors were paired in analyses due to lack of independence. Transmitter data were paired based on how long both transmitters lasted within a pair, so amount of data used (measured in days) was identical for individuals within a pair, but varied among pairs (16.0 ± 5.8, range 6–24 days, $n = 21$ pairs).

Sexual differences in parental effort were analyzed using paired t-tests, with the data divided into early and late chick rearing. To examine the relationships among individuals and pairs in their activities early in the chick-rearing period, simple correlations were used to measure chick provisioning and breeding site attendance within each sex and within pairs. We used ANOVAs and post-hoc Fisher's Partial Latin Square Design (PLSD, Zar 1996) to compare year-to-year differences in total rates of provisioning and breeding site attendance, as well as how much time a pair spent together at their crevice (during week 2 of chick rearing), as possible indicators of food availability within a breeding season (Cairns 1987). A condition index based on the regression of body mass on tarsus length (Jones and Montgomerie 1992) was measured and compared to male and female parental effort (total rates of provisioning and attendance). We used a Chi-square test to examine whether males and females were likely to provision at different times of the day. The two activity periods (see Jones 1993b) provided the basis for dividing the day into four 6-hr periods: 00:00 to 06:00, 06:00 to 12:00, 12:00 to 18:00, and 18:00 to 24:00 hr. In all cases, statistical significance was $P < 0.05$ and means are presented ± SE, unless otherwise stated.

We calculated the time a chick spent unattended at the breeding site during early chick rearing for each pair. A chick was considered unattended if it was alone for greater than 1 hr. Interannual comparisons were made with a Kruskal-Wallis test.

CHICK GROWTH

To determine whether the transmitters on adults affected their chick's growth, we used Mann-Whitney U-tests to compare fledging variables (mass and wing length) and linear growth rates of mass with a sample of chicks whose parents were handled but not fitted with transmitters. We also examined whether parental effort or the time a chick spent unattended were related to measures of chick quality (linear growth rates of mass and mass and wing length at fledging) using Spearman rank correlations. Nests in which chicks were measured for growth were checked every two days near anticipated hatch date, and chick age was estimated to within one day based on appearance (Jones 1993b). Chicks were then measured every three days until they departed from their crevice; in most cases exact fledging dates were known. The length of the linear growth phase was estimated from regression residuals to be from 6 to 24 days of age (see Fraser et al. 1999 for detailed chick growth methodology). We used ANOVAs to compare interannual variation in fledging mass, age, and linear growth rates of mass (n = 56 chicks).

COLONY-LEVEL PRODUCTIVITY

In 1996, we measured productivity on Main Talus by checking crevices approximately every seven days throughout each breeding season (n = 66). In 1997 and 1998, we checked crevices every four days to obtain more precise estimates of hatching and fledging dates (n = 82, 70). These crevices were not used in the telemetry study or for chick growth. We used the midpoint between visits to estimate hatching and fledging dates and the even-numbered Julian date when an even number of days occurred between visits. We defined hatching and fledging success as the proportion of eggs that hatched and chicks that fledged, respectively. For all crevices, chicks were considered fledged if they were 26 days or older upon disappearance. Overall colony productivity was the product of hatching and fledging success, but we tested crevice productivity (i.e., crevices that fledged chicks vs. crevices that neither hatched nor fledged chicks) among years with a chi-square analysis.

CHICK VULNERABILITY EXPERIMENT

In 1998 we experimentally measured the vulnerability of young, unattended chicks by placing plasticine models of chicks in Crested Auklet crevices that were occupied in previous years, but were unoccupied during the 1998 breeding season. The chick models were made of gray or brown plasticine and equipped with black glass eyes, an artificial bill, and black "down" made from yarn. They were approximately 6 cm high by 10 cm long, similar to a 5-day-old chick. Thirty-one models were placed in individual crevices for 5-day intervals during each of three time periods: (1) pre–hatching (25–30 June), (2) peak hatching (7–13 July), and (3) post hatching (21–26 July). We used three time periods because the number of prospecting adults varied throughout the breeding season (Jones 1993b). At the end of each trial, we collected the models and recorded the number of bill marks (pokes, scrapes, and bites) from Crested Auklets and other auk species. For comparison, we collected bill marks on plasticine from captured Crested and Least (*A. pusilla*) auklets and from Horned Puffins (*Fratercula corniculata*). Between each period we smoothed over the various mutilations incurred in the previous period. We compared the number of marks a model incurred for each period using a repeated measures ANOVA.

PREY DELIVERED TO CHICKS

To quantify sexual differences in prey species delivered to chicks, we collected food samples from male and female Crested Auklets during each of the three study years. Crested Auklets prey on zooplankton, predominantly euphausiids and copepods (Bédard 1969b), and chick meals are carried in an esophageal pouch (Piatt et al. 1990). Adults were captured in noose carpets on our study plot (a different sample of birds than was used in the telemetry study) as they arrived at the colony, and the contents of their esophageal pouches was collected. Afterward each bird was measured, sexed, banded, and released. We visually estimated the percentage of the food load that was recovered (some food was invariably lost), weighed the fresh sample, and preserved it in 70% ethanol.

To quantify prey consumption, individual prey items from all taxa except euphausiids were counted. The average mass for copepods was obtained based on preserved single-taxon food samples. For the rare items (e.g., crab megalopa) we calculated average mass from all individuals from each year. Euphausiid mass was calculated by subtracting the total mass of the counted taxa

from the total fresh mass. In the majority of the food samples collected, we were unable to identify euphausiids to genus or count them because few were whole and most were broken down into small pieces (head and tail were missing, presumably removed when the euphausiid was captured); thus the above method provided us with an estimate of the relative proportions of prey items in each food sample. So that each food sample was not weighted more heavily than any other based on original mass, we used aggregated mass in our statistical tests, which is the proportion of each prey type by mass for every sample (Duffy and Jackson 1986, Swanson et al. 1974) and provide an average value for each prey type based on these proportions (Table 1).

The two main prey items (euphausiids, a shrimplike crustacean, and *Neocalanus cristatus*, a calanoid copepod) differed in size. Euphausiids were up to 32 mm long (*Thysanoessa* spp.), and *N. cristatus* was 5–9 mm long (Newell and Newell 1977, Gardner and Szabo 1982). Consequently, our primary interest was in male-female diet differences for these two main prey items. To test for male-female differences, we created a ratio of euphausiids to *N. cristatus* for each sample (aggregated mass; $n + 1$ to adjust for zeros), then ran Mann-Whitney U-tests for sex differences within each year. Prey load size is predicted to increase as chicks age. To test whether males and females brought in similar prey loads throughout the chick-rearing season, we used a two-way ANOVA on prey load size with sex and chick rearing stage as factors. The chick-rearing stages were divided into food samples collected during the hatching period for the colony, and food samples collected after the last chick in the colony hatched (see Fraser et al. 1999 for breeding chronology). We did this because chick age was unknown for adults from whom food samples were collected. To test whether there were differences among years in the relative proportions of the two main prey items, we used a chi-square test on the number of samples that had more euphausiids than copepods (Statview 2002).

RESULTS

Crested Auklets did not appear to be adversely affected by the transmitter; they walked, flew, and behaved normally. In all 14 instances when we saw radio-tagged birds arriving at their crev-

TABLE 1. Taxonomic composition (mean ± SE aggregate percent by mass) of chick food loads for male and female Crested Auklets from 1996 to 1998.

	1996			1997			1998		
	Male (n = 23)	Female (n = 46)	Total[a]	Male (n = 33)	Female (n = 39)	Total	Male (n = 29)	Female (n = 70)	Total
Euphausiids	78.2 ± 7.5	79.3 ± 5.0	78.9 ± 4.2***	66.3 ± 6.7	46.7 ± 6.2	55.7 ± 4.7	64.6 ± 6.1	41.7 ± 3.3	48.3 ± 3.1
Copepods									
Neocalanus cristatus	16.7 ± 7.2	16.3 ± 4.8	16.4 ± 4.0***	27.7 ± 6.6	39.7 ± 6.2	34.2 ± 4.5	34.0 ± 6.0	56.0 ± 3.1	49.7 ± 3.0
N. plumchrus	1.1 ± 0.9	2.8 ± 2.0	2.2 ± 1.3	4.1 ± 3.1	11.7 ± 3.3	8.2 ± 2.3	1.1 ± 0.4	1.7 ± 0.8	1.5 ± 0.6
Amphipods									
Parathemisto pacifica	0.19 ± 0.1	0.3 ± 0.2	0.3 ± 0.1	1.2 ± 0.5	1.6 ± 1.0	1.4 ± 0.6	0.3 ± 0.2	0.5 ± 0.2	0.4 ± 0.1
Other[b]	3.8 ± 2.8	1.4 ± 1.1	2.2 ± 1.2	0.7 ± 0.2	0.3 ± 0.2	0.5 ± 0.2	0.03 ± 0.003	0.2 ± 0.1	0.1 ± 0.1
Ratio, euphausiids: N. cristatus[c]	1.7 ± 0.11	1.7 ± 0.08		1.5 ± 0.1+	1.2 ± 0.09+		1.3 ± 0.1**	0.97 ± 0.04**	

[a] Chi-square test for differences between the relative proportions on the number of samples that had more euphausiids than copepods delivered to chicks among years; ***$P < 0.001$.
[b] Crab megalopa, crab zoea, shrimp zoea, larval fish, pteropods, and snails.
[c] Mann-Whitney U-test results for male-female differences in euphausiid to *N. cristatus* ratio for each year; † $P < 0.1$, ** $P < 0.01$.
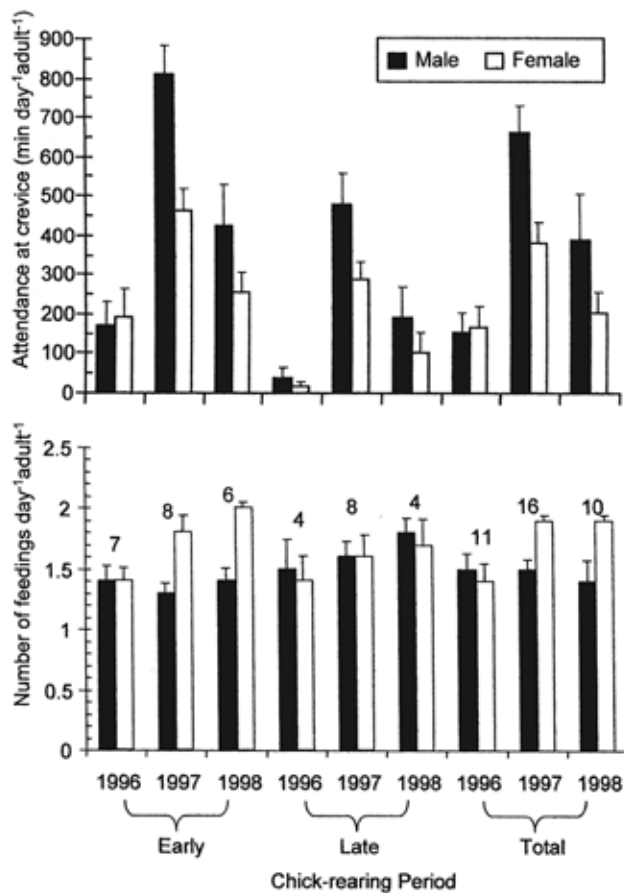
FIGURE 1.   Mean ± SE breeding site attendance and chick-provisioning rates of male and female Crested Auklets at Buldir Island, Alaska. Early and late refer to stages of chick rearing (chicks aged 2–14 days and 15–25 days, respectively). Sample sizes (number of pairs) appear above bars and apply to both breeding site attendance and provisioning.

ices, they had obvious food loads as indicated by a distended esophageal pouch. Our direct observations confirmed that the provisioning and breeding site attendance rates, indicated by radio-telemetry, were a realistic reflection of activity at the crevices.

MALE AND FEMALE PROVISIONING AND BREEDING SITE ATTENDANCE

Males and females had significantly different rates of provisioning and breeding site attendance early in chick rearing (provisioning: $t_{1,20}$ = 3.1, P < 0.01; attendance: $t_{1,20}$ = −2.9, P < 0.01) and different rates of breeding site attendance in late chick rearing ($t_{1,15}$ = −2.9, P = 0.01; Fig. 1). In 1997 and 1998, males attended their chick 75% and 90% more than females, and females provisioned their chick 33% and 36% more often than males. In 1996, however, we found no sexual differences in breeding site

attendance or provisioning rates (Fig. 1). We observed no sexual differences in parental provisioning late in chick rearing ($t_{1,15}$ = −0.7, P = 0.5). We found significant differences among years (early and late chick rearing combined) in breeding site attendance ($F_{2,18}$ = 13.4, P < 0.001, Fisher's PLSD: 1996 vs. 1997, P < 0.001; 1996 vs. 1998, P > 0.15; and 1997 vs. 1998, P < 0.001), but not for provisioning ($F_{2,18}$ = 2.9, P = 0.08).

Male condition was, overall, positively related to breeding-site attendance (r = 0.59, n = 21, P = 0.004), but not to provisioning (r = 0.18, n = 21, P = 0.4). Females in better condition did not attend or provision at higher rates (r = 0.2, P = 0.3; r = −0.15, P = 0.5, respectively, n = 21). Total female provisioning and breeding-site attendance rates were positively correlated (r = 0.5, n = 21, P = 0.04). Rates of male provisioning and breeding site attendance showed a nonsignificant negative trend (r = −0.3, n = 21, P = 0.1).

PAIR RELATIONSHIPS

Total male breeding-site attendance was significantly and positively related to total provisioning of their mate (r = 0.5, n = 21, P = 0.02), and total rates of breeding-site attendance were positively correlated between the sexes (r = 0.6, n = 21, P = 0.005). Chick provisioning rates were not correlated between members of a pair, nor was male provisioning correlated with female breeding-site attendance (r = 0.01, n = 21, P = 0.9 for both tests). Pairs spent highly variable amounts of time together in their crevice. During week 2 of chick rearing, members of a pair spent very little time together in the nest crevice in 1996 (n = 21, mean = 25.3 ± 12.9 min day^{-1}), compared to 1997 (mean = 332.3 ± 73.5 min day^{-1}) and 1998 (mean = 107.8 ± 33.3 min day^{-1}; $F_{2,20}$ = 9.9, P = 0.001). In early chick rearing, chicks were left unattended longer in 1996 (mean = 848.5 ± 85.2 min day^{-1}, n = 7) than in 1997 (mean = 524.3 ± 42.8 min day^{-1}, n = 8) or 1998 (mean = 570.3 ± 63.2 min day^{-1}, n = 6; Kruskal-Wallis test, H = 10.3, P < 0.01).

The consistent pattern of male and female parental care during chick rearing was particularly striking (Fig. 2). If a female spent the night in the crevice, 89 ± 7% (early chick rearing; mean ± 95% CI calculated on a per-female basis, years combined) and 98 ± 5% (late chick rear-
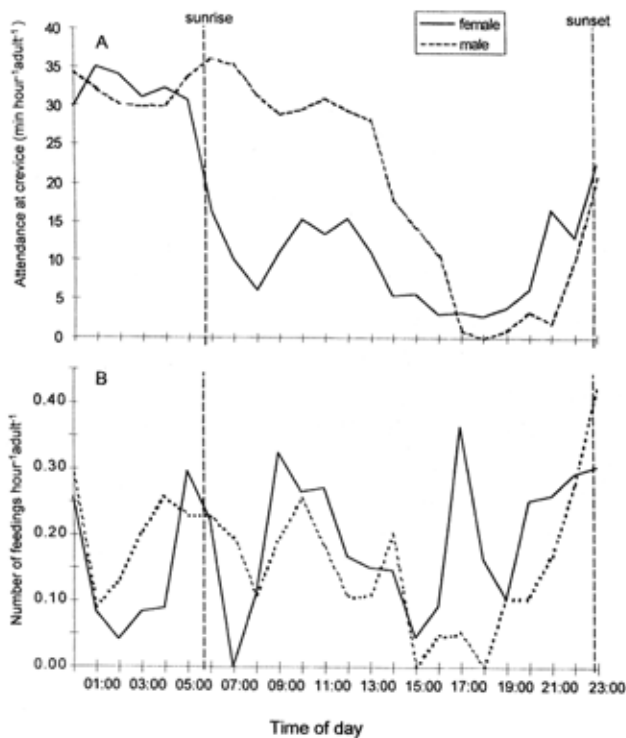
FIGURE 2. Diurnal patterns of male and female Crested Auklets ($n = 21$ pairs; means of three breeding seasons) for (A) breeding-site attendance and (B) provisioning during week 2 of chick rearing.

ing) of the time she left the colony between 05:00 and 07:30 and usually returned sometime during the morning activity period (10:00 to 14:00; see Jones 1993b) or in the early evening (18:00 to 21:00). On the other hand, if a male spent the night in the crevice, he left the colony in the morning only 14 ± 8% of the time during early chick rearing. However, this pattern changed markedly and males were likely to leave the colony in the morning (71 ± 22%) late in chick rearing.

Overall sexual differences in provisioning were not significantly related to time of day for either early or late chick rearing (early: $\chi^2_3 = 5.3$, $P = 0.2$; late: $\chi^2_3 = 1.2$, $P = 0.8$). However, females provisioned chicks more often during the early evening (18:00 to 21:00) than did males (77% greater frequency; Fig. 2). Thirteen percent of adults captured in crevices at night (12:30–04:00) had a food load in their esophageal pouch, which supports our nighttime provisioning scores (Fig. 2).

CHICK GROWTH

We found no differences in linear growth rate or fledging variables between chicks with parents with and without transmitters (Mann-Whitney

U-tests, all $U \geq 153$, all $P > 0.05$). All chicks with radio-tagged parents survived to fledging. Total male or female parental effort was not significantly correlated with selected chick growth variables (linear growth rate in mass, fledging mass, and wing length, all $P > 0.05$). Nor were any of the chick growth variables correlated to combined (male + female) parental effort (all $P > 0.05$). Also, the amount of time that chicks were left unattended early in chick rearing was not related to the growth or to the status of the chick at fledging (linear growth rates, fledging mass, and wing length, all $P > 0.05$). We found no differences among years for chick fledging mass (all $P \geq 0.9$), fledging age (all $P \geq 0.1$), or linear growth rate (all $P \geq 0.8$).

COLONY-LEVEL PRODUCTIVITY

We observed no statistical differences in colony-level measures of hatching (1996 = 86%, 1997 = 94%, 1998 = 89%; $\chi^2_2 = 2.5$, $P = 0.3$) or fledging success (96 = 70%, 1997 = 81%, 1998 = 85%; $\chi^2_2 = 4.3$, $P = 0.1$) among the three study years. Productivity was lower for 1996 (60%) compared to 1997 or 1998 (both years = 76%), although this difference was not significantly different ($\chi^2_2 = 5.1$, $P = 0.08$). However, we had several other reasons to believe that 1996 was different from the other two years (see Discussion), so we combined 1997 and 1998 and found productivity to be significantly lower in 1996 ($\chi^2_1 = 5.0$, $P = 0.03$).

CHICK VULNERABILITY EXPERIMENT

Young chicks left unattended appeared to be vulnerable to attacks. During the period of our study we found three dead chicks (all under 1 week old) that had injuries consistent with an attack by an adult (i.e., peck marks breaking the skin and evidence of trampling). Before and during hatching 81% of the clay chicks in our model chick experiment were poked, scraped, or bitten, and after hatching 87% had these marks ($n = 31$ models). There was a significant difference in the number of marks that the models incurred during each trial (means: pre-hatch = 19.4 ± 4.4; peak hatch = 11.9 ± 3.3; post-hatch = 36.8 ± 6.9 marks per trial; repeated measures ANOVA, $F_{2,31} = 9.6$, $P < 0.001$). Most of the marks on the models were pokes or scrapes, which matched marks obtained from Crested Auklets captured on the study plot. In three instances,

the bites on the models were much bigger and were probably delivered by a puffin.

PREY DELIVERED TO CHICKS

Males and females provisioned chicks with food loads of similar mass, and the mass of the load increased as the season progressed (two-way ANOVA; sex: $F_{1,236} = 0.4$, $P = 0.5$; chick-rearing stage: $F_{1,236} = 8.6$, $P = 0.003$; sex × chick rearing stage $F_{1,236} = 0.9$, $P = 0.3$). During the hatching period (i.e., younger chicks), parents provisioned chicks, on average, with 9.6 ± 0.5 g of food; after the hatching period (i.e., older chicks), chicks received 11.8 ± 0.6 g of food.

Crested Auklets brought in four main prey types: euphausiids, two species of copepods (*N. cristatus*, *N. plumchrus*), and the hyperiid amphipod *Parathemisto pacifica*. We found significant differences among years in the delivery of prey items (Table 1). Notably, adults delivered more *N. cristatus* and fewer euphausiids in 1997 and 1998, than in 1996. Males brought in a higher ratio of euphausiids to *N. cristatus* than females in 1997 and 1998. In 1996, there was no significant difference between the sexes in the ratio of euphausiids to *N. cristatus* delivered to chicks.

DISCUSSION

Male and female Crested Auklets had distinct roles in parental care of young chicks, with males attending more and females investing more time in provisioning. Males in better body condition had higher rates of nest site attendance; however, body condition in females was not related to any of the variables measured. Total rates of breeding-site attendance and provisioning were positively correlated among females, but not among males. Within-pair behavior was also correlated: males that attended more had females that provisioned more, and male and female breeding site attendance were positively related.

MALE AND FEMALE CHICK PROVISIONING AND BREEDING SITE ATTENDANCE

Why did males spend more time with small chicks than females? Our model chick experiment suggested that chicks may require protection from aggressive conspecifics, and that the likelihood of attacks increased after peak hatching. Although Crested Auklet chicks begin to develop homeothermy four to five days post-

hatching and may gradually require less attendance thereafter (Jones 1993b), it appears there may be a risk in leaving young chicks unattended. This was supported by our findings of dead, attacked chicks in their natal crevices. Crevice breeding sites may be limited at Buldir, and aggressive competition for sites occurs both within and between species (Knudtson and Byrd 1982, Jones 1993b). Because males are more aggressive than females (Jones and Hunter 1999), and have larger and stronger bills (Jones 1993a), they might be better at guarding their chick from prospectors.

The requirement to guard chicks may involve a trade-off for parents in poor food years. In years when food is scarce, parents must make the decision to guard their young chick or to leave it unattended while they forage at sea, but in these years prospecting birds attend the colony in lower numbers (Jones 1992), and the risk of attack to unattended chicks is thus likely to be lower.

Both males and females are likely to benefit from adopting specific parental roles (Gowaty 1996). For example, higher rates of breeding site attendance may aid in the maintenance of crevice ownership, supported by our observations that males, not females, retain the crevice when a pair splits up (Fraser 2000). Similarly, higher rates of chick provisioning may allow females more opportunities to forage for themselves.

Subtle male-female differences in parental care appear to be the norm rather than the exception for seabirds, even though in all species both sexes contribute substantially. For example, female Black Skimmers (*Rynchops niger*), Common Murres (*Uria aalge*), and Atlantic Puffins (*Fratercula arctica*) fed their chick more, while males maintained the breeding site more (Burger 1981, Wanless and Harris 1986, Creelman and Storey 1991). In many seabirds males are slightly larger and more aggressive than females (e.g., Black Skimmers, Atlantic Puffins, and Razorbills [*Alca torda*]; Burger 1981, Creelman and Storey 1991, Wagner 1999).

Curiously, we observed no relationships between parental effort and fledging mass, wing length, or linear growth rate. One reason might be that the best measure relating parental care to breeding success is chick survival to adulthood, which we were unable to measure. Alternatively, chick growth is often constrained by intrinsic factors when food is abundant (Gaston 1985,

Cairns 1987), and food availability may not have been limiting during our study (with the exception of 1996; see below).

Unlike the other two years of our study, in 1996 we observed no male-female differences in provisioning rates, breeding-site attendance, or prey delivery. We also recorded lower rates of chick feeding and breeding-site attendance, lower productivity, lower adult mass, a higher likelihood of young chicks being unattended, and a higher likelihood of nest abandonment after handling in 1996 (Fraser et al. 1999, Fraser 2000, this study). Furthermore, *N. cristatus* is an important prey item for Crested Auklets on Buldir, and 1996 had the lowest frequency of occurrence and percent mass of this species in prey samples that had been recorded in five breeding seasons (1994–1998, Fraser et al., unpubl. data). Cairns (1987) identified five variables that reflect food availability: activity budgets, colony attendance, breeding success, chick growth, and adult survivorship, and concluded that colony attendance and activity budgets were better measurements of prey availability for seabirds. Of these variables we considered four (activity budgets [provisioning], colony attendance, breeding success, and chick growth), and we conclude that food availability was limited in 1996. Lower prey availability in 1996 may have resulted in no differences in parental care between male and female Crested Auklets.

Uttley (1992) credited variability in male vs. female breeding-site attendance to food availability in Arctic Terns (*Sterna paradisaea*). In a non-food-limited colony, male Arctic Terns shared incubation equally, but brooded less and fed young chicks more than females. In a food-limited colony, however, males contributed less than females during the incubation stage, but both sexes shared equally in brooding and feeding.

PREY DELIVERED TO CHICKS

Bédard (1969b) found no evidence that male and female auklets consumed different prey during incubation and chick rearing at St. Lawrence Island, Alaska (62°N latitude); however, he also reported that Crested Auklets delivered primarily euphausiids. Two differences between copepods and euphausiids may affect the rates they are consumed by males vs. females: (1) copepods have a higher lipid component compared to euphausiids (Lee et al. 1972, Lee 1975), and

(2) copepods are less able to swim against the current than euphausiids (Bédard 1969b). Our study has shown sexual differences in the proportions of prey items consumed during the chick-rearing period; in 1997 and 1998 females delivered more copepods than euphausiids to their chicks; while males delivered more euphausiids. This suggests that females may have foraged in different locations or depths than males, foraged at different times of the day, or taken copepods over euphausiids for nutritional reasons. It is possible that these behavioral differences are specific to Buldir due to the unique physiographic features surrounding the island (Springer et al. 1996); however, further knowledge of zooplankton distributions in relation to auklet foraging locations around Buldir and elsewhere in the Aleutians would be required to confirm this.

Male-female differences in prey consumption and foraging strategies have been noted in other seabirds. Wagner (1997) reported sexual differences in prey delivered to chicks for Razorbills and suggested that it resulted from feeding-niche partitioning. Razorbill males, like Crested Auklets, have a deeper bill than females (Wagner 1999), and engage in aggressive displays more often than females (Wagner 1996). Weimerskirch et al. (1997) found that female Wandering Albatross (*Diomedea exulans*) were more likely to bring their chick oceanic prey species, whereas males were more likely to bring prey from the shelf edge. Male provisioning constituted 50% more energy than female provisioning. In contrast to our findings, Williams (1990) found sexual differences in Gentoo Penguin (*Pygoscelis papua*) diets only in low food years.

MANAGEMENT IMPLICATIONS

Variation in annual food availability can have profound impacts on the variance in breeding success for seabirds. Adult attendance at the crevice appeared to be the most sensitive indicator of food availability; however, monitoring attendance using telemetry is expensive and time consuming. Adult attendance may be a more practical indicator of food availability for open nesters such as kittiwakes (*Rissa* spp.) and murres (*Uria* spp.), but not for crevice or burrow-nesting seabirds. Provisioning was slightly, but not significantly, lower in 1996, which suggests that this measure is not a good index of food availability. Among the Crested Auk-

chick growth variables we measured, little variability was evident among the three study years (Fraser et al. 1999, this study), indicating that for this species, chick growth variables are also a poor reflection of local prey availability. Productivity appeared to be a better measure of food availability (Fraser et al. 1999, Fraser 2000) than chick growth or provisioning, and was the most practical variable to assess. However, productivity has limited usefulness as an index because it only measures adults that engage in breeding, and in poor food years many adults may not even attempt breeding. While monitoring of auklet productivity may aid in following local trends in prey availability, continued efforts should be made to understand the complex interactions of prey availability and the above variables by collecting long-term, multifaceted data sets whenever possible.

ACKNOWLEDGMENTS

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