

NIGHTLY COLONY ATTENDANCE PATTERNS OF PROVISIONING CASSIN'S AUKLET *PTYCHORAMPHUS ALEUTICUS* ARE CONSISTENT AND SYNCHRONOUS

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ABSTRACT

MCFARLANE TRANQUILLA, L., RYDER, J.L., BLIGHT, L.K., O'HARA, P.D. & BERTRAM, D.F. 2020. Nightly colony attendance patterns of provisioning Cassin's Auklet *Ptychoramphus aleuticus* are consistent and synchronous. *Marine Ornithology* 48: 263–272.

We conducted a multi-year (1999–2001) radio telemetry study to determine patterns of colony attendance among breeding Cassin's Auklets *Ptychoramphus aleuticus* during the chick-rearing period on Triangle Island in British Columbia, Canada. A total of 1625 detections were obtained for 80 individual birds (24–28 birds per year), each detected 20.3 times on average. We found that colony attendance (arrival times, departure times, in-burrow shift duration) and foraging trip duration (i.e., time away from the colony) were remarkably synchronous among individuals and years. On average, birds arrived in a pulse after darkness, with 67% of returns between 23h15 and 00h15 and a peak (22% of all returns) between 23h30 and 23h45. Birds departed synchronously en masse before sunrise, with 86% of departures between 03h15 and 04h15 and a peak (38% of all departures) between 03h45 and 04h00. Overall, parents visited the colony every 19.8 hours (median) and stayed for roughly four hours during the chick-rearing period. At the beginning of the season, female foraging trip duration was longer than that of males, though this decreased with day of year, suggesting that females may aim to recover condition immediately following egg production via increased foraging time. Most breeders routinely visited the colony every night despite the risk posed by avian predators. Understanding patterns of colony attendance is important, given changing ocean conditions and prey availability in the vicinity of the world's largest colony for this species.

Key words: Nocturnal behaviour, predation risk, timing of breeding, Alcidae, radio telemetry, synchrony, tagging effects

INTRODUCTION

Life histories of long-lived seabirds are characterized by consistent traits that include small clutch size and variable-distance foraging trips from a central place nesting colony. Smaller seabirds, including several of the Alcidae, generally return to the colony only at night to provision their young. This nocturnal colony attendance has likely evolved in response to the threat posed by avian predators (Gaston & Jones 1998), which may often breed on or be attracted to seabird colonies (Kaiser 1989, Nelson 1989, Nelson 1990). Life history theory (Stearns 1992) dictates that, for long-lived species, individuals should be reluctant breeders because they must safeguard their own survival over current reproductive efforts in order to save themselves for future breeding opportunities, thus maximizing lifetime reproductive output (Erikstad *et al.* 1998, Hipfner *et al.* 2006). Consequently, incubating seabirds may spend less time at the colony when foraging conditions are poor (Ronconi & Hipfner 2009, Blight *et al.* 2010). During the chick-rearing

phase, parents may similarly adjust colony attendance to maintain their own body mass, altering provisioning rates and thus affecting chick fledging mass and success (Weimerskirch *et al.* 1994, Ballard *et al.* 2010, but see Wischnewski *et al.* 2019).

Here we report on colony attendance behaviour for breeding Cassin's Auklets *Ptychoramphus aleuticus* at the world's largest colony for this species: Triangle Island in British Columbia, Canada has more than one million individuals, or about 55% of the global population (Rodway 1991, Rodway *et al.* 1992, Rodway & Lemon 2011, Environment Canada 2013, COSEWIC 2014). During incubation and in the first few days of the early chick-rearing period, Cassin's Auklets are present in their nesting burrows day and night (Ainley *et al.* 2011). Once nestlings can thermoregulate (*ca.* five to six days after hatch; Manuwal 1974), parents leave them alone in the burrow so that both adults can forage simultaneously at sea. Chicks are fed nocturnally via regurgitation, with diet in British Columbia consisting primarily of zooplankton and fish

(Bertram *et al.* 2001, 2009). While there is long-standing evidence that adults make provisioning trips to the colony each night until the chick fledges (Manuwal 1974; Ainley *et al.* 1990, 2011; Domalik *et al.* 2018), our study adds to the understanding of these nightly patterns of attendance. Using radio transmitters and a data collection computer (DCC), we recorded nightly visits to determine details of colony attendance behaviour by chick-rearing auklets. Measurements included arrival time, time in burrow, departure time, and time at sea during the nestling period. This work was carried out over three consecutive years as part of a larger-scale program studying breeding seabirds' movements (Boyd *et al.* 2008, Bertram *et al.* 2017b) and productivity (Bertram *et al.* 2017a).

STUDY AREA AND METHODS

We captured and tagged 112 Cassin's Auklets at the colony in West Bay, Triangle Island, Canada (50°52'N, 129°05'W; Fig. 1). The study spanned three years, with birds captured on 06–19 June 1999 ($n = 39$), 23 May–19 June 2000 ($n = 35$), and 14–23 May 2001 ($n = 38$). Capture dates were timed to coincide with the midpoint of the 45-day chick-rearing period, based on the distribution of lay dates in each particular year. Captures occurred at night (sunset and

sunrise on 01 June were ~21h35 and ~05h20, respectively), with breeding adults either removed from burrows by hand ($n = 63$) or captured with a stationary pheasant net ($n = 49$) as they returned to the colony to deliver food-loads to nestlings (Boyd *et al.* 2000, Ryder *et al.* 2001, McFarlane Tranquilla *et al.* 2005). The breeding status of captured adults was confirmed by the presence of food in their gular pouch and/or the presence of a chick in the occupied burrow. None of the radio-tagged birds was paired to another tagged bird. Sex was assigned to adults using bill-depth measurements (male = bill depth > 9.9 mm; female = bill depth < 9.7 mm; Knechtel 1998). We did not assign sex when bill depth was 9.7–9.9 mm. Based on bill-depth measurements, there were 13 birds of unknown sex in our sample.

Each captured bird was fitted with a radio transmitter (2.2 g, 45-day lifespan, ATS Model 392, Advanced Telemetry Systems, Isanti, Minnesota, USA) that was secured with a subcutaneous anchor following protocols described by Newman *et al.* (1999) and modified as per Boyd *et al.* (2000, 2008). A telemetry receiver (Model R4000, Advanced Telemetry Systems), an H-antenna, and a remote recording system (Data Collection Computer II, Model D5041, Advanced Telemetry Systems) were set up at the

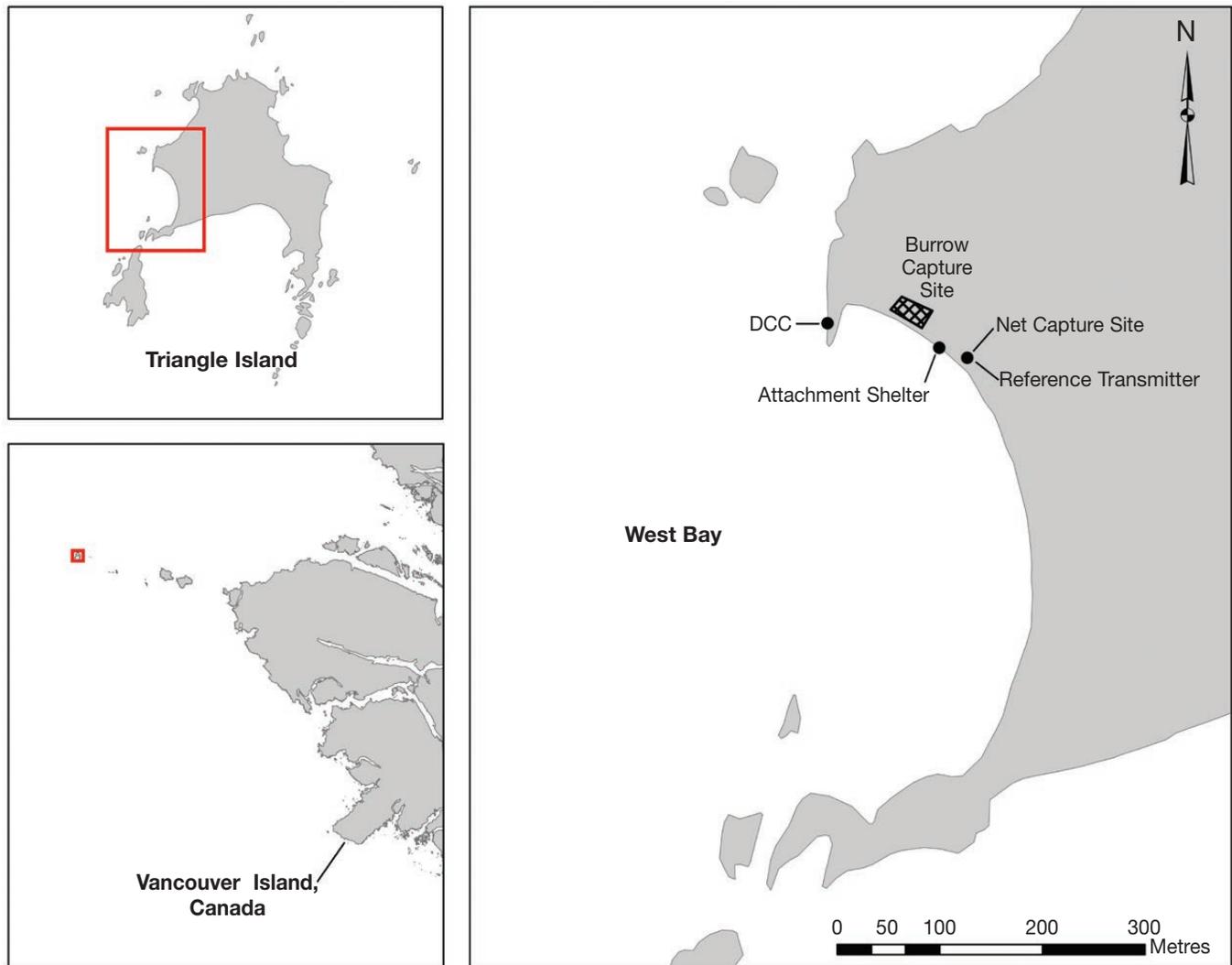


Fig. 1. Map of Triangle Island, British Columbia, Canada (50°52'N, 129°05'W) showing the locations of the capture sites, reference transmitter, and Data Collection Computer (DCC) in West Bay.

northwestern end of West Bay to monitor nocturnal attendance by tagged birds (Fig. 1).

The DCC was active continuously (14 June to 07 July 1999, 24 May to 07 July 2000, 25 May to 30 July 2001; Boyd *et al.* 2008) following capture and during the chick-rearing period in all years, with these date ranges constituting our study period for each respective year. The DCC recording period overlapped some fledging events, especially in 2001, when it was active for longer. It was programmed to record radio frequencies at intervals of 5–10 seconds to monitor arrival times, and, following the detection of a specific frequency, to reduce the scan time to 15-minute intervals until the individual departed the colony. This approach was taken to preserve DCC memory and battery life. Thus, arrival times were exact to the minute, but departure times were exact to only 15-minute intervals; likewise, colony attendance shifts and foraging trip durations were exact to only 15-minute intervals. Thus, for the purposes of our analyses, we assigned departure times as the start time of each 15-minute interval. Because arrival and departure times were recorded at different intervals, we also assigned arrival times into 15-minute bins to match the temporal resolution of the departure times. Thus, we calculated durations of colony attendance and foraging trips based on 15-minute intervals in arrival and departure times.

Radio frequencies that had fewer than four detections ($n = 19$) were excluded from our analyses. This excluded tagged birds that deserted their nests at the beginning of the tagging period and those that visited occasionally (~once/month). This resulted in a total of 80 individuals ($n = 24$ in 1999; $n = 28$ in 2000; $n = 28$ in 2001) with which to investigate colony attendance. A reference frequency from a transmitter at the colony was recorded every 15 minutes during all years of the study to confirm that the equipment was functioning properly (Boyd *et al.* 2000). We assumed that the breeding birds we detected returning to the colony always returned to their burrows to feed and brood chicks (as opposed to other activities such as prospecting or resting on the surface) but did not verify this behaviour for individual study birds.

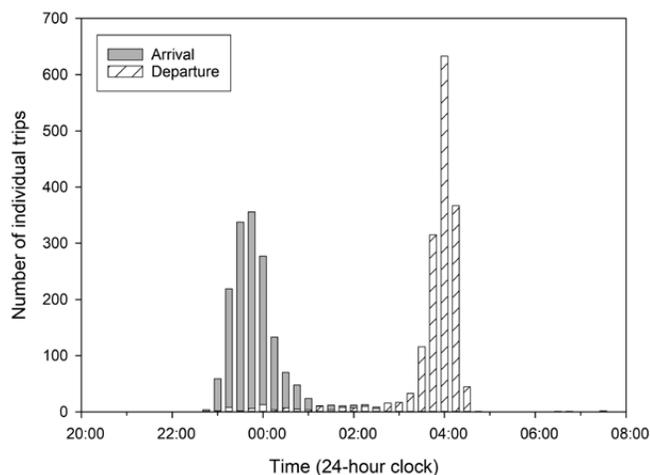


Fig. 2. Cassin's Auklet daily arrival and departure times at the Triangle Island breeding colony (1999–2001 pooled, $n = 1\,323$ trips; x-axis shows 20h00–08h00). Arrival and departure times are overlain on each other, and anomalous foraging trips at the far tail ends of distributions were removed for visual clarity.

Data were non-normally distributed. We tested for distributions using the R package “fitdistrplus” (Delignette-Muller & Dutang 2015, R Core Team 2019; Appendix 1) and found that the gamma distribution was the best fit for arrival and departure times and for foraging trip and colony shift durations. To fit arrival times, departure times, colony shift duration, and foraging trip duration separately, we used generalized linear mixed-effects models (GLMMs) with gamma distributions (inverse link function) and individual as the random effect (“lme4” package in R; Bates *et al.* 2015). These GLMMs tested the data for variability associated with Julian day (i.e., day since 01 January of each year), sex, year, and sex \times year as covariates, then they were reduced via backwards elimination of variables using P values as a guide; P values smaller than 0.05 were considered significant. We tested for the integration of variability among individuals as a random effect using Akaike information criterion (AIC, reported in model outputs) and likelihood ratio tests (lrtest function in the R package “lmer”; Zeileis & Hothorn 2002). We found that in all cases, AIC was considerably lower for models with the random effect included, and removal of the random effect resulted in a highly significant likelihood ratio test ($P < 0.0001$). GLMM results are presented with Wald (type III) chi-square tests (maximum likelihood) and numerator degrees of freedom. There are currently no reliable means of estimating denominator degrees of freedom for a GLMM. We also tested for differences among years with Tukey-adjusted post-hoc comparisons (“lsmeans” package in R; Lenth 2016), and again, we considered all P values smaller than 0.05 to be significant. We estimated intercepts at Julian day 145, which is the approximate beginning date of our study each year.

For graphing purposes only, anomalous colony shift and foraging trip durations at the tail ends of the distribution were removed to display the data more clearly. These removals were not part of our data analyses.

RESULTS

Daily colony arrival and departure times

We recorded a total of 1 625 detections for 80 individual birds, each of which was detected 20.3 times on average (range: 4–44 times per individual; see Appendix 2 for raw data). When years were pooled, the most arrivals (mode $n = 357$; 22%) at the colony occurred between 23h30 and 23h45, with 67% of arrivals occurring between 23h15 and 00h15 ($n = 1\,094$; Fig. 2). Departures were more synchronous than arrivals, and most (mode $n = 612$; 38%) occurred between 03h45 and 04h00, with 86% (mode $n = 1\,397$) of the observations occurring between 03h15 and 04h15 (Fig. 2).

Nocturnal arrival times at the colony (Table 1, Fig. 3) varied with Julian day inconsistently among years (Table 2; intercepts at Julian day 145: Wald chi-square = 36.9, $df = 2$, $P < 0.0001$; slopes: Wald chi-square = 21.3, $df = 2$, $P < 0.0001$) and sexes (Table 2; intercepts at Julian day 145: Wald chi-square = 58.3, $df = 1$, $P < 0.0001$; slopes: Wald chi-square = 62.1, $df = 1$, $P < 0.0001$). Post-hoc comparisons (Table 2) revealed that arrival times began later at night in 2000 than in the other two years and did not change with Julian day, whereas arrival times were increasingly delayed in both 1999 and 2001 until there was no significant difference among years by the end of the observation period (approx. Julian day 187, Fig. 3). While controlling for variation with Julian day, we found that arrival was generally earlier for males at the beginning of the

study year (Table 2; Wald chi-square = 58.3, $df = 1$, $P < 0.0001$) and increased by Julian day (Table 2) until statistical parity with female arrival times—which did not vary with Julian day (Table 2)—was achieved at the end of the observation period (Fig. 3).

Early morning departure times from the colony (Table 1, Fig. 3) also varied by Julian day inconsistently among years (Table 2; Wald chi-square = 24.9, $df = 2$, $P < 0.0001$), but unlike arrival times, annual variability in departure times was consistent between sexes (both intercept at Julian day 145 and slope, $P > 0.6$). Post-hoc comparisons revealed that departure times were remarkably consistent with Julian day for both 1999 and 2000 (Table 2, Fig. 3)

but began earlier in 2001 and increased until statistical parity with year 1999, but not year 2000.

Duration of colony shifts and at-sea foraging trips

Parent Cassin's Auklets spent an average of $4\text{h}21\text{m} \pm 00\text{h}05\text{m}$ (SE) per night in the burrow with their chick (range: $00\text{h}11\text{m}$ to $28\text{h}26\text{m}$; Fig. 4), with 80% of colony shifts lasting 3.0–5.5 h. Cassin's Auklets were away from the colony on foraging trips lasting $20\text{h}38\text{m} \pm 00\text{h}07\text{m}$ on average (median: $19\text{h}48\text{m}$, range: $01\text{h}31\text{m}$ to $48\text{h}39\text{m}$), with 80% of trips ($n = 1\ 291$) lasting 19.0–21.5 h (Fig. 5).

TABLE 1
Annual mean arrival and departure times, and mean and range (min–max) of colony shift and foraging trip durations for data pooled among Cassin's Auklets breeding at Triangle Island

Year	<i>n</i> (birds)	Time ^a		Colony Shift Duration		Foraging Trip Duration	
		Mean Arrival ± SE	Mean Departure ± SE	Mean ± SE	Range	Mean ± SE	Range
1999	24	23h24 ± 0h01	03h40 ± 0h01	4h49m ± 0h11m	0h16m–27h58m	20h11m ± 0h11m	18h35m–46h12m
2000	28	00h00 ± 0h03	03h34 ± 0h02	4h24m ± 0h10m	0h11m–28h26m	21h20m ± 0h14m	6h12m–48h10m
2001	28	23h39 ± 0h04	03h16 ± 0h04	4h00m ± 0h05m	0h12m–27h30m	20h13m ± 0h10m	1h31m–47h38m

^a Time in 24-hour clock; SE = standard error

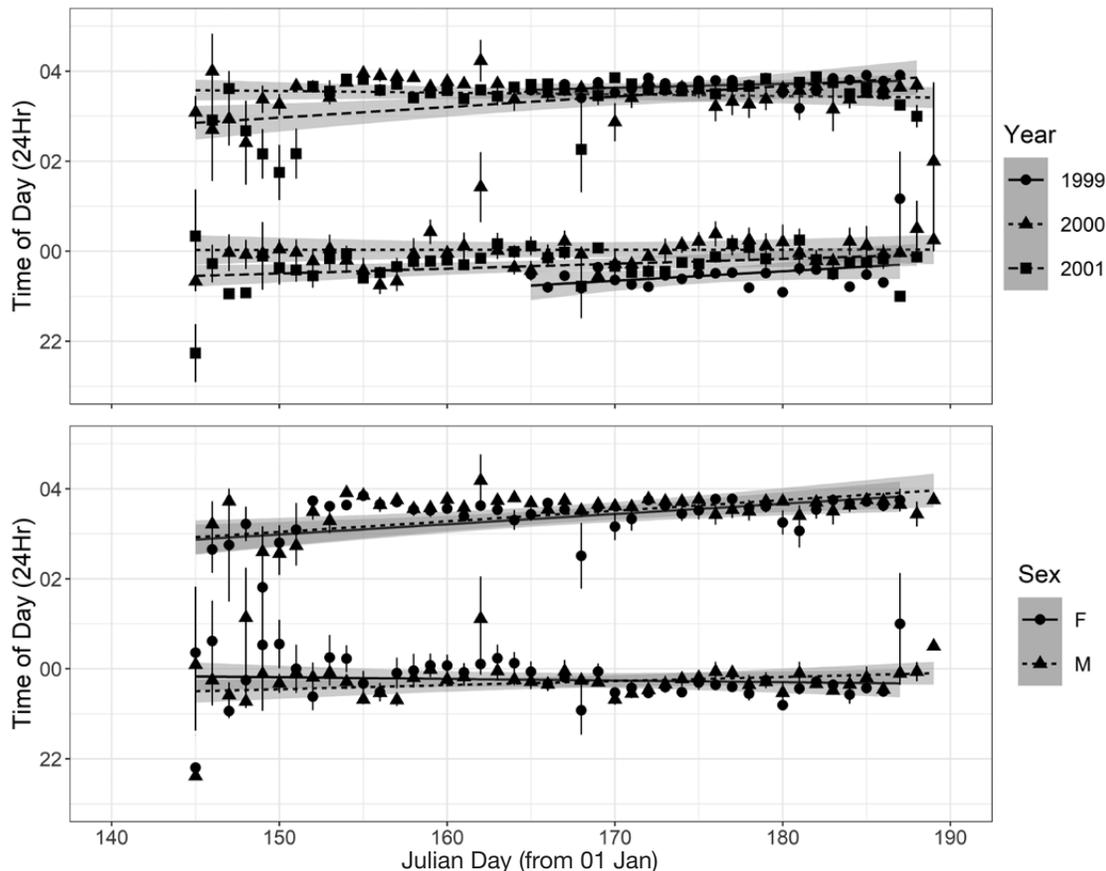


Fig. 3. Mean (\pm SE) daily arrival and departure days by sex and year for Cassin's Auklets at Triangle Island. Lines represent linear regressions (see Table 2); departures are represented by the top line and arrivals by the bottom line in each panel.

Colony shift duration (Table 1) varied with Julian day inconsistently among years (Table 3; intercepts at Julian day 145: Wald chi-square = 27.7, $df = 2$, $P = 0.0001$; slopes: Wald chi-square = 18.8, $df = 2$, $P < 0.0001$) and sexes (Table 3; intercepts at Julian day 145: Wald chi-square = 4.81, $df = 1$, $P = 0.028$; slopes: Wald chi-square = 4.30, $df = 1$, $P = 0.038$). Post-hoc comparisons revealed that colony shift duration (Table 3) started similarly among years but decreased with Julian day, particularly in years 1999 and 2000.

Males generally started with longer colony shifts but decreased more rapidly with Julian day than females.

Foraging trip duration (Table 1) also varied with Julian day inconsistently among years (Table 3; intercepts at Julian day 145: Wald chi-square = 49.0, $df = 2$, $P < 0.0001$; slopes: Wald chi-square = 43.5, $df = 2$, $P < 0.0001$) and sexes (Table 3; intercepts at Julian day 145: Wald chi-square = 26.5, $df = 1$, $P < 0.0001$; slopes:

TABLE 2
Estimated intercepts (at Julian day 145) and rates of change with Julian day for both arrival (year and sex) and departure times (year only)^a

Arrival Time						
Year	<i>n</i>	Intercept (Julian Day 145)		Rate of Change (min/d)		
		(Estimate ± SE)	Post-hoc	(Estimate ± SE)	Significance	Post-hoc
1999	395	23h06 ± 0h08	a	0.54 ± 0.07	$P < 0.0001$	a
2000	638	00h12 ± 0h12	b	-0.12 ± 0.18	$P = 0.51$	b
2001	591	23h30 ± 0h10	a	0.80 ± 0.16	$P < 0.0001$	a
Sex						
Female	546	23h48 ± 0h09	NA	0.04 ± 0.09	$P = 0.65$	NA
Male	767	23h24 ± 0h08	NA	0.78 ± 0.12	$P < 0.0001$	NA

Departure Time						
Year	<i>n</i>	Intercept (Julian Day 145)		Rate of Change (min/d)		
		(Estimate ± SE)	Post-hoc	(Estimate ± SE)	Significance	Post-hoc
1999	395	03h24 ± 0h10	a	0.40 ± 0.22	$P = 0.068$	a
2000	638	03h30 ± 0h11	a	-0.22 ± 0.41	$P = 0.88$	a
2001	591	02h36 ± 0h08	b	2.30 ± 0.40	$P < 0.0001$	b

^a Arrival time (24-hr clock) parameters were estimated for year controlling for sex-associated variation, and sex-associated parameters were estimated controlling for annual variability. P values were Tukey-adjusted for multiple comparisons. Post-hoc comparisons were also based on Tukey-adjusted P values (see Study Area and Methods). SE = standard error. n = sample size (number of detections). NA = not applicable.

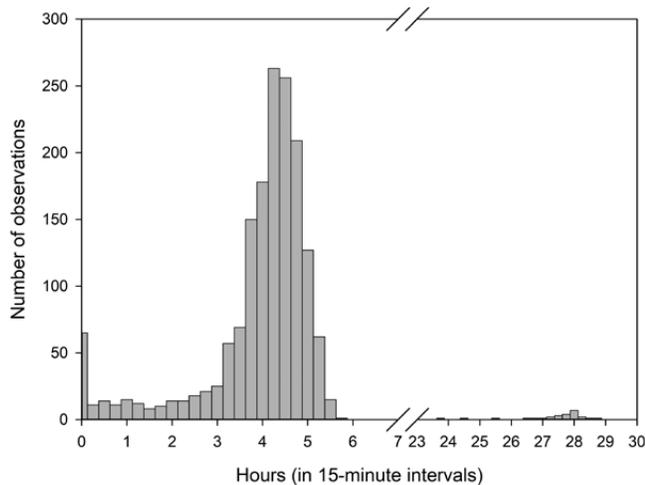


Fig. 4. Time spent in burrow (colony shift duration) of Cassin's Auklets at Triangle Island (1999–2001, years pooled). Data are represented in 15-minute intervals, with each bar centered on the interval being represented (e.g., the bar at 1 represents 1h00m–1h15m).

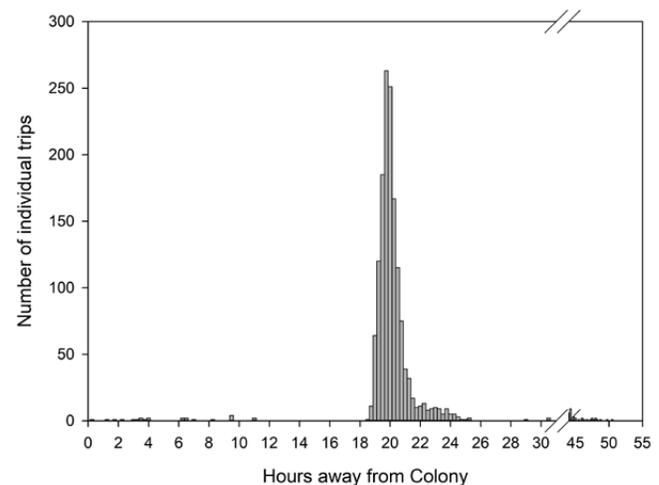


Fig. 5. Foraging trip duration, measured as time away from colony, of Cassin's Auklets at Triangle Island (1999–2001, years pooled). Data are represented in 15-minute intervals, with each bar centered on the interval being represented (e.g., the bar at 1 represents 1h00m–1h15m).

Wald chi-square = 30.7, $df = 1$, $P < 0.0001$). Post-hoc comparisons (Table 3) revealed that foraging trip duration was longer in 2000 and 2001 than 1999, but decreased rapidly with Julian day, while duration increased with Julian day in 1999. At the end of the study periods there was no difference in foraging trip duration among years ($P > 0.05$). Female trip duration was longer than that of males at the beginning of the year, but decreased with Julian day, while for males, trip duration remained constant throughout the year. At the end of the study periods, females generally had shorter

foraging trips than males (females: 19h06m \pm 1h03m; males: 23h48m \pm 1h35m).

Anomalous colony shift durations lasting longer than six hours (natural cut-off in the data) were 14–28 hours long (63% were 28 hours long; Fig. 6A), with the bird in the burrow for a full day being the most common shift anomaly. Anomalous foraging trip durations that lasted longer than a 24-hour (i.e., one day) window occurred in all years, and they were 2–25 days long, with a two-day

TABLE 3
Estimated intercepts (at Julian day 145) and rates of change with Julian day for both colony shift duration and foraging trip duration (year and sex)^a

Colony Shift Duration						
Year	<i>n</i>	Intercept (Julian Day 145)		Rate of Change (min/d)		
		(Estimate \pm SE)	Post-hoc	(Estimate \pm SE)	Significance	Post-hoc
1999	395	5h46m \pm 0h46m	a	-2.46 \pm 0.86	$P = 0.0043$	ab
2000	604	4h47m \pm 0h28m	a	-2.59 \pm 0.45	$P < 0.0001$	b
2001	562	3h56m \pm 0h16m	a	-0.61 \pm 0.41	$P > 0.05$	a
Sex						
Female	519	4h18m \pm 0h21m	NA	-1.16 \pm 0.49	$P = 0.019$	NA
Male	740	5h24m \pm 0h22m	NA	-2.62 \pm 0.48	$P < 0.0001$	NA

Foraging Trip Duration						
Year	<i>n</i>	Intercept (Julian Day 145)		Rate of Change (min/d)		
		(Estimate \pm SE)	Post-hoc	(Estimate \pm SE)	Significance	Post-hoc
1999	371	18h30m \pm 01h02m	a	2.05 \pm 1.29	$P = 0.0001$	a
2000	579	29h48m \pm 03h07m	b	-12.00 \pm 3.36	$P = 0.0001$	b
2001	536	26h12m \pm 02h03m	b	-5.90 \pm 2.56	$P = 0.021$	b
Sex						
Female	491	26h30m \pm 2h01m	NA	-9.31 \pm 1.88	$P < 0.0001$	NA
Male	708	23h12m \pm 1h25m	NA	0.77 \pm 1.94	$P > 0.05$	NA

^a Colony shift and foraging trip parameters were estimated for year controlling for sex-associated variation, and sex-associated parameters were estimated controlling for annual variability. P values were Tukey-adjusted for multiple comparisons. Post-hoc comparisons were also based on Tukey-adjusted P values (see Study Area and Methods). SE = standard error. n = sample size (colony shift and foraging trip durations that were estimable from detections in Table 2). NA = not applicable.

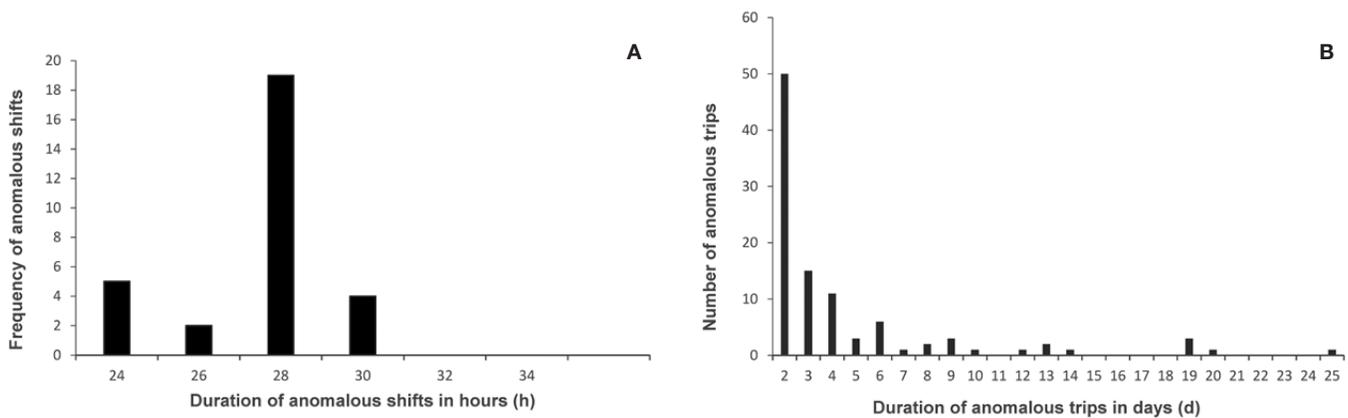


Fig. 6. Frequency of anomalous (A) colony shifts (number of hours) lasting more than the average six hours; and (B) foraging trips (number of days) lasting more than the average 24 hours among Cassin's Auklets (1999–2001, years pooled).

trip being the most frequent by far among anomalous trips (50% were two days long; Fig. 6B).

DISCUSSION

Provisioning Cassin's Auklets arrived at and departed from the colony quickly and synchronously at night. Arrival and departure patterns showed remarkable consistency among years and generally among individuals. Thus, foraging trip duration and return to the burrows each night was equivalent to a single chick-provisioning event per day for most adults. Some birds, however, spent about one day in their burrow (Fig. 4), presumably brooding their chick, and departed the following night instead (see also anecdotal details on variation, below). Most adult birds (67%) feeding chicks arrived in the one-hour period between 23h15 and 00h15 (i.e., arrival rate increased ~1.5 h after sunset) and most (86%) departed between 03h15 and 4h15, about 1–1.5 h before sunrise. These results are consistent with an earlier radar-based study in West Bay, which reported that Cassin's Auklet activity at the colony began approximately 1.5 hours after sunset and ended at least 15 minutes before sunrise, although that study did not quantify individual behaviour or numbers of arriving and departing breeders (Bertram *et al.* 1999). Similarly, GPS loggers subsequently applied to Cassin's Auklets at this same site described average arrival time as 23h10 (107 min post-sunset) and average departure time as 04h23 ("shortly before sunrise"). That same study recorded an average foraging trip duration of 1134 min (18.9 h; Domalik *et al.* 2018). Our results also show qualitatively similar arrival and departure patterns to those described by Manuwal (1974) in his early study of this species elsewhere in its range, at Southeast Farallon Island (SEFI), California, USA. He observed that, during the breeding season, most birds arrived within two hours of dark, and a steady trickle of auklets left the colony from 24h00 to 04h30, with the rate of departure accelerating sharply at 04h30, about 90 minutes before sunrise. At the annual scale, Ainley *et al.* (1990) showed that yearly SEFI patterns of colony visitation were linked to interannual variation in ocean conditions and prey availability.

Natural selection for predator avoidance has likely had a strong influence on the life history and nocturnal colony attendance behaviours of this small burrow-nesting seabird (Ainley *et al.* 1990). As Triangle Island supports the world's largest nesting population of Cassin's Auklets, as well as having populations of other seabirds, this location attracts predators such as Peregrine Falcon *Falco peregrinus* and Bald Eagle *Haliaeetus leucocephalus*, both of which nested at the colony during the study period. Peregrine Falcons on North America's northwestern coast specialize in seabird prey and are known to depredate Cassin's Auklets at Triangle Island (JLR, LKB, DFB pers. obs; Hipfner *et al.* 2011); they also affect the migratory behaviour of other birds (e.g., shorebirds; Ydenberg *et al.* 2004) by presence alone. A pair of Peregrine Falcons is capable of capturing and consuming hundreds of seabirds in a breeding season (up to 1000 per peregrine family per year based upon studies of Ancient Murrelets *Synthliboramphus antiquus*, a seabird similar in size to the Cassin's Auklet; Nelson & Myres 1976, Nelson 1990).

Despite visitation patterns being remarkably consistent overall, there were small but significant differences associated with year and sex. Males started the breeding season with longer colony shifts, but their shift durations decreased with day faster than those for females (Table 3). For data pooled between sexes, colony shift duration decreased over the breeding season for both 1999 and 2000, but

not for 2001. Concurrent demographic studies on Triangle Island indicated differential effects of ocean climate variation on male and female adult survival patterns for Cassin's Auklet. In years of unfavorable ocean climate (low prey production), female adult annual survival is halved (to 0.44 ± 0.1) but that of males remains roughly constant (0.75 ± 0.03 ; Morrison *et al.* 2011). In contrast, in favorable ocean climate years, female adult annual survival is higher (0.84 ± 0.05) than for males (0.75 ± 0.03 ; Morrison *et al.* 2011). Our study was conducted during a period when survival was higher for females than for males, so it is plausible that even in some years of higher prey availability, females may need to regulate their survival via shorter visits to the colony to increase the time available for foraging and self-provisioning. Regulating survival may be particularly important for females towards the beginning of the season—as demonstrated in our study—following energetically costly egg production.

Even seemingly small differences in the amount of foraging time could be important for small seabirds like Cassin's Auklet, which have high energetic needs, particularly when breeding: adults consume 67% of their body mass in euphausiids per day (Hodum *et al.* 1998). Parents consistently provision nestlings with two feeds per night (one feed per parent) when chicks are between 10 and 49 days old in both good and poor years for prey on Triangle Island (Hedd *et al.* 2002). Our study was conducted during a succession of three good years when nestling growth rates were average to very high (FOWG 2002) and when fledging success and mass were consistently high (Hipfner 2008). Foraging trip duration was remarkably conservative, with small yet significant variation among years and between sexes (Table 3) reflecting the variability found in arrival and departure times (Table 2). Males began with shorter foraging trip duration, which did not change significantly with time over the season, and females began with longer trip duration, which decreased with time.

While the arrival/departure times and colony shift/foraging trip durations were overwhelmingly consistent overall, the raw data do reveal a few interesting instances of more than one visit per night by an individual parent, some variation in colony shifts, and a wide range of numbers of days between colony visits. In three years, only three birds were detected coming to the colony twice on the same night. Several individuals did colony shifts shorter than one hour, and a few birds did extra-long colony shifts (mostly staying a full day in the burrow; Fig. 6A). Notably, one individual in 2000 did eight consecutive double-shifts (two nights in burrow, each lasting 27–28 hours) and then was at sea for 19–20 hours (a regular at-sea foraging trip interval) between each double-shift. Occasional, long foraging trips (most of which lasted two to four days; Fig. 6B) were relatively common among radio-tagged birds and were distributed throughout the chick-rearing period. However, this individual variation comprised events that were tails of a distribution with a large spike equivalent to one visit per day per individual (Figs. 4, 5).

Effects of tagging on auklet behaviour

Immediately after capture and radio tagging, several birds in each year temporarily disappeared for longer than a regular foraging trip duration, or occasionally stayed in the burrow for much longer than a regular colony shift duration. Over the three-year study, there were 30 anomalously long first foraging trips or first colony shifts in the days immediately after tagging. These birds then resumed normal colony shift (~4-hour) and foraging trip

(~20-hour) durations for the rest of the chick-rearing period. Conversely, four of the birds we tagged (one in 1999, three in 2001) appeared to abandon the colony after a few detections (4–6 colony shifts and then gone for the rest of the season). This result is mirrored by aerial telemetry results from Boyd *et al.* (2008), in which these same tagged Cassin's Auklets were noted as having long periods of absence from the colony or were detected at sea but not at the colony. The effects of tagging individuals with devices are not inconsequential and can include short-term effects such as colony abandonment, reduced chick-provisioning rates, reduced chick growth rates, mate compensation (Ackerman *et al.* 2004, Robinson & Jones 2014, Symons & Diamond 2019), and longer foraging trip durations (Paredes *et al.* 2005). Longer-term physiological effects may be present when year-round devices are deployed, such as elevated baseline or stress-induced corticosterone levels (Elliott *et al.* 2012, Quillfeldt *et al.* 2012) and reduced return rates or survival in following years (Schacter & Jones 2017, Pakanen *et al.* 2020). Given that alcids seem particularly vulnerable to the energetic cost of carrying even a small device (Vandenabeele *et al.* 2011) and that subcutaneous anchors are more likely than other attachment methods to have an adverse effect (Barron *et al.* 2010), it is likely that some of the anecdotal individual variation we saw in this study was a result of device effect. We recommend future studies include controls to directly address such potential tagging effects.

CONCLUSIONS

The telemetry data presented here contribute unique insights to Cassin's Auklet colony attendance patterns and foraging behaviours during the nestling provisioning stage, the most energetically demanding period for seabirds (Elliott *et al.* 2013). We demonstrate that the majority of Cassin's Auklets on Triangle Island routinely visit the colony every night despite ongoing risk of predation. Parental colony visitation during chick rearing is remarkably consistent at this site. Whether colony visitation patterns ultimately affect survival, through predation risk, energy expenditure requirements, or other variables, requires further study. However, it seems reasonable to expect that some trade-off exists between consistent chick-provisioning rates and adult survival, particularly in years of poor foraging conditions such as those resulting from climate-related ocean warming around Triangle Island (Bertram *et al.* 2017a). Alternatively, it may be that future breeders respond to ocean warming by attempting to maximize their own survival, meaning that colony visitation frequency could decline, with implications for chick production. Tracking of fine-scale colony attendance patterns, consistent with the approach we demonstrate here, may provide additional insight into mechanisms of seabird responses to climate change. New and emerging GPS technologies can provide increasingly detailed information on seabird movements and behaviour, facilitating the increased understanding of seabird colony attendance patterns that may be required to manage effects of both ocean warming and the resultant changes to prey species composition and condition.

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