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ORIGINAL PAPER

Small interannual variability in the body mass of a seabird with high flight costs

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Abstract

Seabird parents during chick rearing is hypothesized to regulate body mass to reduce flight costs and invest energy in current reproduction. Alcids have 2−4 times higher wing-loading and higher flight costs than other seabirds. In particular, rhinoceros auklets *Cerorhinca monocerata* (RHAU) carry the heaviest meals among alcids despite its medium-size, therefore, we expected that they might be more likely to keep their body mass small and within a narrow range during chick rearing. We examined between-breeding stage and interannual variations in RHAU body mass using 27-year monitoring data, then tested whether the interannual variation shown by the coefficient of variation (CV) in body mass during chick rearing was smaller than in other seabirds, and if their body lipid stores were smaller. RHAU during chick rearing have 15−20 g lower body mass, corresponding to 5−7% decrease of flight costs, than those during incubation. We found that CV of body mass in RHAU (1.4) was smaller than those of 10 other seabird species (1.7−7.5), while CVs in provisioning metrics, such as meal mass, chick growth, fledgling mass, and fledging success, were the largest or second largest. RHAU body lipid stores during chick rearing (3.8−4.0%) was also smaller than six other species (5.7−9.5%). Results suggest that chick-rearing RHAU maintained a narrow range of body mass with minimum body lipid stores, possibly because of their greater wing-loading and heavier meals. Such constraints on body mass regulation might affect their variable investment in their chicks under environmental variability, as shown large variation in provisioning metrics.

Keywords Body lipid stores · *Cerorhinca monocerata* · Adaptive mass loss · Species comparison · Alcids · Flight costs

Introduction

Life-history theory predicts that avian parents regulate their own body mass to maximize their life-time fitness (Clutton-Brock 1991; Stearns 1992). Avian parental body mass varies mainly with body lipid mass (Niizuma et al. 2001b, 2002; Jacobs et al. 2011) which is an important factor determining their survival (Oro and Furness 2002; Harding et al. 2011). Body mass also determines flight costs through changes in wing loading. Avian parents during chick rearing, in particular, face to accept extra flight costs to carry meals for chicks although the meal mass is different by species. They are hypothesized, therefore, to reduce their body mass between the incubation stage and the chick-rearing stage to save on flight costs and carry meals for their chicks (Nordberg 1981; Moreno 1989). However, there are interannual variations in adult body mass during chick rearing, though not as large variations as in provisioning metrics (including meal mass and chick growth) (Piatt et al. 2007). Inter-annual changes in prey availability driven by climate change or variability in environmental condition might induce these variations (Weimerskirch et al. 2001; Gaston and Hipfner 2006a). The extent of the interannual variation in body mass of each species may be associated with species-specific flight costs since body mass largely determines flight costs (Niizuma et al. 2001b; 2002). Because species working with higher flight costs may have as narrow a body-mass range as possible to save flight costs, such species may show only small interannual variability.

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Seabird parents likely face life-history tradeoffs given the extensive fluctuation in the marine ecosystem (Cairns 1987; Piatt et al. 2007). Alcids, a seabird family with 2–4 times the wing loading of others (Fig. 1), have to flap their wings continuously at high frequencies to produce sufficient lift, so they must accept the highest concomitant flight costs (Pennycuick 1987; Elliott et al. 2013). Therefore, they may have narrower ranges of adaptive body mass during chick rearing so as to carry heavy meals. In particular, among alcids, rhinoceros auklets *Cerorhinca monocerata* despite their medium size carry the heaviest meals in their bills for their chicks (Gaston and Jones 1998). Their body mass variability, therefore, is expected to be smaller than other seabirds including alcids because of their higher wing loading when they are carrying meals to the chicks. Indeed, the body mass of parent rhinoceros auklets was found to be about 30 g (5.3–5.5%) lower during chick rearing than during the incubation stage, suggesting that they save on flight costs during chick rearing (Niizuma et al. 2002). By comparing annual variability in body mass during chick rearing in rhinoceros auklets with that of other seabirds including alcids, we can test the hypothesis that the species retains its body mass within a narrow range during chick rearing when they have higher flight costs.

To discuss the inter-species difference in body mass variability and flight costs, we must consider inter-species differences in body lipid stores (body lipid mass ratio to body mass). In seabirds, changes in adult body mass during breeding mainly reflect the change of body lipid stores (Niizuma et al. 2001b, 2002; Jacobs et al. 2011). If the species is sensitive to save flight costs, then it will retain as little as possible body lipid stores during chick rearing, but such low body lipid stores may force them to maintain body mass, because to ensure their survival they are unable to lose any more body lipids.

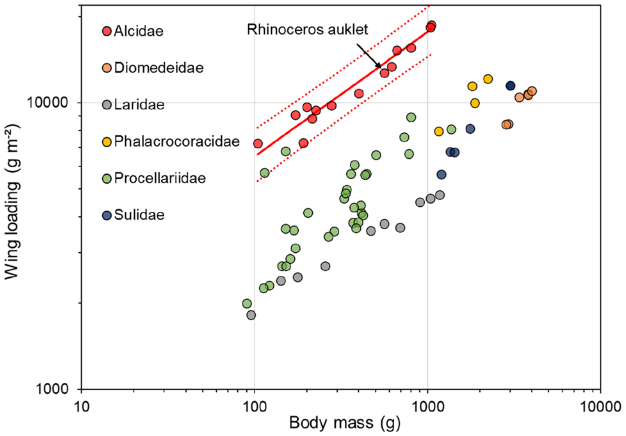

Fig. 1 Seabird wing loading (WL) in relation to body mass (BM). Data from Pennycuick (1987) and Spear and Ainley (1997). Colors indicate each seabird family. Each point mean species. The solid line on alcidae points is the regression line estimated by Phylogenetic generalized least squares (PGLS) model (log10(WL) = 0.4356962* log10(BM) + 2.9417711); The dotted lines indicate lower and upper of 95% confidence intervals of the model. The PGLS model that assumed Brownian motion model of evolution was fitted to log10 WL as response variable, and log10 BM as predictor. See Supplementary Information 2 for the method and summary of PGLS model

In this study, first, we analyzed the adult body mass and the provisioning metrics (meal mass, chick growth, fledgling mass and fledging success) of rhinoceros auklets during chick rearing. We used long-term monitoring data collected at Teuri Island, located in the Sea of Japan off Hokkaido, between 1994 and 2020. More specifically, we tested (1) whether the body mass of adults during chick rearing was smaller than during incubation, and (2) whether annual mean parental body mass during chick rearing varied simultaneously with provisioning metrics, (3) whether the provisioning metrics and annual mean parental body mass during chick rearing correlated with an environmental variability index which coincides with the variation in availability of forage fish for rhinoceros auklets, and then we calculated (4) the amplitude of interannual variation in annual mean adult body mass and provisioning metrics by coefficients of variations (CVs). In addition to the data at Teuri Island, we also analyzed data collected at Daikoku Island, located in the Pacific Ocean off Hokkaido, between 2014 and 2017, to confirm the consistency in inter-annual and -seasonal body mass variation in the species among colonies (above (1) and (4)).

Second, by species comparison we further tested two hypotheses, (5) that interannual variability in adult body mass during chick rearing in rhinoceros auklets with high flight costs is smaller than other species of seabirds, and (6) that the small body-mass-variability of this species is associated with their small body lipid store during chick rearing. To compare the CVs for rhinoceros auklets obtained in (4) with those for other seabird species including alcids, we used data from published literature. Also, we compared the body lipid stores (body lipid mass ratio to body mass) during chick rearing among seabirds including rhinoceros auklets using information from the literature.

Methods

Study species

Rhinoceros auklets are a medium-sized alcid (body mass: 500–600 g) breeding widely in the mid-latitudes of the North Pacific. They feed on forage fish by making 0–50 m deep dives 225–580 times a day (Kuroki et al. 2003). They lay one egg annually, both parents take turns every other day to incubate it for over 45 days (Gaston and Jones 1998). After hatching, both parents feed their chick once per night for up to 40–60 days until fledging (Gaston and Jones 1998;

Takahashi et al. 2001). Their meal mass (ca. 30 g load^{-1}) is the heaviest among alcids (Gaston and Jones 1998). During chick rearing, they travel up to 160 km from their colonies to forage (Kato et al. 2003; Wilkinson et al. 2018; Okado and Watanuki 2023) by beating their small wings at 8.9 Hz (Kikuchi et al. 2015). Their trip duration (i.e., provisioning frequency) is basically 1 day (Wilkinson et al. 2018; Sato et al. 2022), but sometimes longer than 2 days possibly because of distant foraging under conditions of poor prey availability (Takahashi et al. 1999, 2001; Deguchi et al. 2010).

Several studies in California, British Columbia, and northern Japan have shown that rhinoceros auklets increase provisioning metrics during chick rearing inter-annually with the increase in prey availability driven by interannual or -decadal environmental variability (Hedd et al. 2006; Thayer and Sydeman 2007; Borstad et al. 2011). At Teuri Island, Hokkaido, Japan, rhinoceros auklet change their provisioning metrics inter-annually possibly in relation to changes in the forage fish community that may be associated with local ocean currents at the annual scale and environmental variability at the decadal scale (Takahashi et al. 2001; Watanuki et al. 2009, 2022). Variability in parental body mass, and whether it varies in line with provisioning metrics, has not been examined.

Fieldwork

We conducted fieldwork at rhinoceros auklet colonies on Teuri Island in north-western Hokkaido (44° 25′ N, 141° 19′ E) and on Daikoku Island in eastern Hokkaido (42° 57′ N, 144° 52′ E) (Fig. 2). Nest burrow numbers were estimated 379,000 on Teuri Island with multiplying average nest burrow density by overall nesting area (Biodiversity Center of Japan 2017), and 77,000 on Daikoku Island with sum of those calculating above estimation by each vegetation type (Okado et al. 2019). For this study, we used data collected on Teuri Island from 1994 to 2020 and on Daikoku Island from 2014 to 2017.

We captured parent rhinoceros auklets landing with meals in their bills at the edge of the colony at the south end of Teuri Island. We caught auklets throughout the chick-rearing stage from mid-May to early August (1994–2020) (see Watanuki et al. 2022 for details). We arbitrarily captured 10 individuals each week by hand or in hand nets during the period 30–120 min after sunset (total 2,400 individuals; range = 52–128 each year, Table S1 and S2). In the same plots, we captured adults without meals during the incubation stage, from mid-April to late-May in 1994, 1996, 2004–2007, 2009–2010 and 2014–2019 (total 490 individuals; range = 14–69 each year, Table S1 and S2). All of the 48 birds caught during the incubation stages in 2004 and 2017 had noticeable brood patches. We assumed therefore that most of the birds caught during the incubation stage in the sampling plot were breeding. We assumed that we did not sample the same individuals repeatedly during the same year given the high density of burrows and large enough sampling area of both colonies (Teuri Island: 1.36 burrows m^{-2}, Biodiversity Center of Japan 2017, c 100 m along 4 m wide road, Daikoku Island: 1.26 burrows m^{-2}, Okado et al. 2019, c 50 m × 50 m). We occasionally re-trapped adults that had been ringed by Japanese Ministry of the Environment on Teuri Island; however, according to records during chick rearing over six years (Okado and Watanuki unpublished), it was very rare to catch individuals repeatedly during the same season (1995, 0/36 individuals; 1999, 0/9; 2000, 0/27; 2002, 0/17; 2003, 1/23; 2004, 0/8). No individuals were re-trapped during the incubation stage in 2010 (0/4 individuals). In addition, we believe that our sample size is large enough to discount individual variation. On capture, we measured the size of external traits using calipers following to Niizuma et al. (1999): bill depth to the nearest 0.1 mm (maximum depth of the bill at the front of the nostril) and head plus bill length to 0.1 mm (distance from the tip of the bill to the rear of the supraoccipital bone). We measured mass to the nearest 5 g using a Pesola spring balance. On Daikoku Island, we captured adults without meals during the middle of the incubation stage during late-May in 2016 and 2017 (total 45 individuals; range = 21–24 each year, Table S1 and S2), and parents carrying meals during the early chick-rearing stage in early July 2014–2016 (total 68 individuals; range = 22–24 each year, Table S1 and S2). We measured their morphometrics as on Teuri Island.

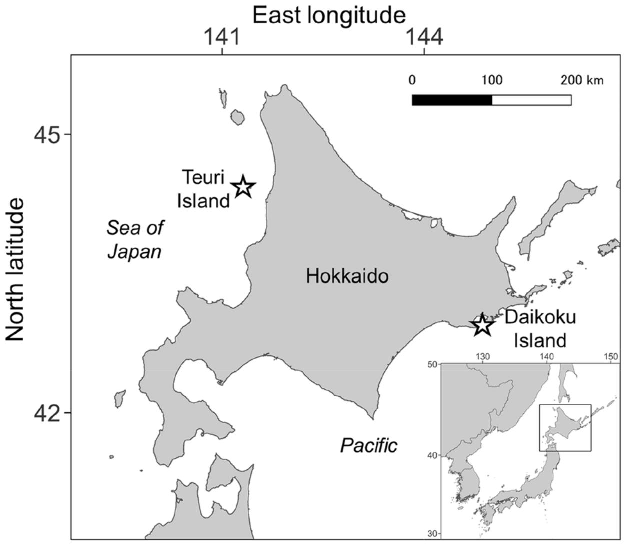

Fig. 2 The study area map. Our study colonies of rhinoceros auklets *Cerorhinca monocerata* are indicated as the stars. The location of the square on the map of Japan (inset)

Body mass

As male rhinoceros auklets are larger than females (Niizuma et al. 1999), body mass was examined separately for males and females. We sexed individuals using a discriminant function relying on bill depth and head plus bill length. The function could sex 95% of individuals correctly (91.2% for males and 100% for females; Niizuma et al. 1999). Annual mean body mass of adults reflects variation in body lipid stores between years (Niizuma et al. 2001a, 2002; Jacobs et al. 2011). For inter-species comparisons we used interannual variation of body mass reported in many previous studies (Table 1). When using annual mean body mass to show interannual variability, we noted that body size may also change between years. In rhinoceros auklets, Niizuma et al. (2001a) provided a method for calculating an index of body-size-corrected body lipid stores (See Supplementary Information 2). We have confirmed that there was a strong linear correlation between the annual mean body mass and annual mean of the index of body-size-corrected body lipid stores across year-colony-breeding stage (Females: Pearson Correlation Test, $t_{44} = 44.017$, $r = 0.99$, $P < 0.001$, $n = 45$, Fig. S1a, Males: $t_{44} = 36.315$, $r = 0.98$, $P < 0.001$, $n = 45$, Fig. S1b, Supplementary Information 2).

Provisioning metrics

We used mean meal mass, chick growth rate, fledgling mass, and fledging success at Teuri Island as provisioning metrics in 1994–2020 (Watanuki et al. 2022). Even though these indices are correlated with each other, we used all four of them for comparison with other species. We collected meals from captured birds for body mass monitoring and weighed the wet mass of each meal. To monitor chick growth, fledgling mass, and fledging success on Teuri Island, 10–84 chicks were weighed by spring balance each year, every 5 days from hatching to fledging (they typically disappeared from their nests after 40 days of age) (Watanuki et al. 2022). Chick growth rate (including those that may have died) was calculated as the slope of the linear regression of mass on age (g per 5 days) between 5 and 20 days for those giving $r > 0.9$. This means that slow-growing individuals were not removed but individuals showing non-linear growth were excluded. Chicks that disappeared after they were 40 days old were defined as fledglings, and the mass of the last day before their disappearance was defined as their fledgling mass. The proportion of chicks fledging, relative to the number that had hatched, was defined as fledging success. As fieldwork was carried out only during the early chick-rearing stage at Daikoku Island, only meal mass data were collected (Okado et al. 2020, 2021).

Environmental variability index

To examine the relationship between environmental variability and provisioning metrics or annual mean adult mass during chick rearing at Teuri Island, we referred the Pacific Decadal Oscillation (PDO) during 1994–2020. The PDO is defined as the leading principal component of monthly sea surface temperature anomalies in the North Pacific, typically north of 20° N. Generally, high PDO values indicate warm conditions in the eastern but cool conditions in the western North Pacific (Mantua et al. 1997; Chavez et al. 2003, but see Kuroda et al. 2020; Litzow et al. 2020). On a decadal scale, the PDO coincides with climatic shifts between warm and cold phases which are associated with changes in fish communities, including forage fish such as anchovy, across the North Pacific (Mantua et al. 1997; Chavez et al. 2003; Tian et al. 2006). During 1994–2020, the PDO index tended to be positive in 1994–2020, negative in 1998–2013 and positive in 2014–2020 (Kuroda et al. 2020; Watanuki et al. 2022). Japanese anchovy *Engraulis japonicus*, a highly profitable prey species for rhinoceros auklets, tends to increase during negative PDO phases (i.e., warm years in North Western Pacific) (Takasuka et al. 2008); rhinoceros auklets at Teuri Island fed more Japanese anchovy to chicks during negative PDO phase (1998–2013) but fed more other forage fish species during positive PDO phase (1994–1997, 2014–2020); the provisioning metrics of rhinoceros auklets were larger in years when Japanese anchovy was the main diet (Watanuki et al. 2022). Given these contexts, we considered the PDO to be an important index of environmental variability that may be related to provisioning metrics or adult mass of rhinoceros auklets. In this study, we used the annual mean of the PDO calculated from monthly data obtained from NOAA (https://www.ncei.noaa.gov/access/monitoring/pdo/, accessed on 20th June 2023).

Statistical analysis of rhinoceros auklet data

The following analyses were performed using R ver 4.1.3 (R Core Team 2022). First, we used ANOVA to test the difference between adult mass during incubation and during chick rearing at each colony, or the difference in adult mass during the incubation or chick-rearing stage between colonies. We validated model assumptions and fit by visually checking the normality of the model residuals, QQ-plot and plot of the residuals versus the fitted values, and confirmed acceptable model fits (Fig. S6). Second, we examined the correlations between annual means of adult mass during chick rearing and provisioning metrics at Teuri Island using the Pearson correlation test ($n = 24$ or 27 years). Third, we examined the correlations between the annual mean PDO and means of adult mass during chick rearing or provisioning metrics at Teuri Island using the Pearson correlation test

Table 1 The coefficient of variation (CV) across years and colonies of adult body mass during chick-rearing, and provisioning metrics in seabirds

Family	Species	Colony	CV of adult body mass				CV of provisioning metrics								References
			Adult mass	*n*	Sampling period	Sample	Meal mass	*n*	Fledging success	*n*	Chick growth rate	*n*	Fledgling mass	*n*	
Alcidae	Rhinoceros auklet *Cerorhinca monocerata*	1	F1.4; M1.4 (1.3)	27	A	X	20.3	27	47.8	27	36.4	27	20.3	24	This study, Watanuki et al. (2022)
	Crested auklet *Aethia cristatella*	1	F1.7; M1.7 (1.9)	8	B	Y	–	–	8.2	8	–	–	–	–	Fraser et al. (1999)
	Atlantic puffin *Fratercula arctica*	1	2.3	6	A	X (3 years) Y (3 years)	30.0	6	10.7	4	21.9	4	8.6	4	Baillie (2001), Baillie and Jones (2004)
		1	2.6	17	A	Z	14.3	38	6.5	31	12.3	34	5.7	37	Harris and Wanless (2011)
	Thick-billed murre *Uria lomvia*	2	3.0	19	A	X	–	–	–	–	–	–	17.8^{b}	19	Gaston and Hipfner (2006a)
	Common murre *U. aalge*	3	3.8	13	C	Z	–	–	28.3	13	–	–	4.2	10	Piatt et al. (2007)
Procellariidae	Short-tailed shearwater *Ardenna tenuirostris*	4	6.4	32	C	Z	–	–	–	–	–	–	11.7^{b}	36	Price et al. (2021)
	Wilson's storm-petrel *Oceanites oceanicus*	1	F2.3; M2.8 (2.5)	4	A	X	3.7	4	26.7	4	–	–	–	–	Quillfeldt et al. (2006), Büßer et al. (2004)
Diomedeidae	Yellow-nosed albatross *Thalassarche chlororhynchos*	1	4.0	7	A	X	6.7	5	–	–	–	–	6.9^{b}	4	Weimerskirch et al. (2001)
Sulidae	Cape gannet *Morus capensis*	1	5.0 ^{a}	8	A	X	–	–	–	–	26.4	8	–	–	Cohen et al.(2014)
Laridae	Black-legged kittiwake *Rissa tridactyla*	3	7.5 ^{a}	15	C	Z	–	–	81.2	13	12.6	12	–	–	Piatt et al. (2007)
Spheniscidae	Adélie penguin *Pygoscelis adeliae*	1	F6.3; M6.6 (5.8)	4	A	X	–	–	37.9^{c}	4	20.6	4	–	–	Watanabe et al. (2020)

We used data from studies where adult mass and provisioning metrics were collected simultaneously for more than four years. Sample size (*n*) is the number of year-colonies. We calculated the CV using annual mean values. The sampling periods were chick-rearing (A), incubation–chick-rearing (B) or late incubating–early chick-rearing (C). The sample included only breeders (X), breeders and non-breeders (Y), or breeders and (possibly) non-breeders (Z). If the annual mean body masses of females and males were available separately, female (F) and male (M) values are shown, and the values for both sexes combined are given in parentheses. In the case of data from multiple colonies where no differences in body size were reported (Gaston and Hipfner 2006a; Piatt et al. 2007; Price et al. 2021), we calculated CV using mean values of all year-colonies data

[a] Calculated from body mass divided by wing length (body size index)

[b] Calculated from body mass during the late chick-rearing stage

[c] The number of chicks fledged against the number of nests during the early chick-rearing stage in the colony

($n = 24$ or 27 years). Fourth, to assess interannual variability in adult mass and the provisioning metrics, we calculated the CVs across years using annual mean values for each colony-breeding stage.

Additionally, to examine the seasonal change in body mass of adult rhinoceros auklets during chick rearing, we performed Linear Mixed Models (LMMs) using the *lmer* function in the *lme4* package (Bates et al. 2015). This analysis was not the main objective of this study but only for reference. LMMs were performed for adults of both sexes during chick rearing on Teuri Island (females $n = 1520$; males $n = 880$), but not for adults during incubation or those on Daikoku Island, because the sampling period there was different by year (Table S2 in Supplementary Information 1), so not appropriate to examine within-stage variation. The full structure of LMMs is described below.

Body mass (assumed Gaussian distribution) ~ Days from mean hatching date in each year (fixed effect, continuous variable) + Year (random effect, categorical variable).

In considering inter-year phenological differences, we used days from the mean hatching date each year between 1994 and 2020 based on Watanuki et al. (2022). We validated model assumptions and fit by visually checking the normality of the model residuals, QQ-plot and plot of the residuals versus the fitted values, and confirmed acceptable model fits (Fig. S5). We assessed the significance of the fixed effects and in LMMs by t-tests using Satterthwaite's method and random effects using the likelihood ratio test, with the LmerTest package (Kuznetsova et al. 2017).

Species comparison of adult mass and provisioning metrics

We referenced studies that had reported annual mean body mass and indices of provisioning metrics for at least 4 years, making it possible for us to calculate the CV (Table 1). In these studies, sampling of adult mass was carried out either during the chick-rearing, incubation–chick-rearing or late incubating–early chick-rearing stages. The samples included either breeders only or breeders and non-breeders. We calculated the CV of adult body mass and provisioning metrics for other species as we did for rhinoceros auklets (Table 1; Table S3 and S4). In cape gannets *Morus capensis* (Cohen et al. 2014) and black-legged kittiwakes (Piatt et al. 2007), adult body mass was divided by wing length. Using our rhinoceros auklet data from two islands, we calculated the CVs of body mass and that of body mass divided by wing length in each sex/stage (Table S1) and confirmed that CVs did not differ greatly between those based on body mass (2.6 for incubating females, 1.4 for chick-rearing females, 2.4 for incubating males, 1.4 for chick-rearing males) and those based on body mass divided by wing length (the same order as previously; 3.4, 2.0, 2.8, 2.1) (Wilcoxon matched-pairs test, $V = 0$, $P = 0.13$). We calculated CV based on data from multiple colonies if the studies described no body size difference among colonies (Gaston and Hipfner 2006a; Piatt et al. 2007; Price et al. 2021). For provisioning metrics for other species, we used reported parameters as similar as possible to those that we used for rhinoceros auklets, such as meal mass, fledging success, chick growth rate, and fledgling mass. For fledging success for Adélie penguins *Pygoscelis adeliae*, we used the number of chicks fledged against the number of nests at the early chick-rearing stage in the colony (Watanabe et al. 2020). For fledgling mass for thick-billed murres *Uria lomvia* (Gaston and Hipfner 2006a), yellow-nosed albatrosses *Thalassarche chlororhynchos* (Weimerskirch et al. 2001), and short-tailed shearwaters *Ardenna tenuirostris* (Price et al. 2021), we used the body mass in the late chick-rearing stage, which was likely before the pre-fledging mass recession.

When comparing species, we should note that CVs were calculated from different numbers of samples ($n = 4-32$ year-colony for adult body mass, Table 1). To assess whether CVs based on different sample sizes were comparable, we conducted two CV simulations with different sample sizes. First, using 27-year-colony data of annual mean body mass of rhinoceros auklets during the chick-rearing stage at Teuri Island, we sampled n year-colony data out of 27-year-colony data and calculated the CV, and repeated this 200 times for each n (4−27). As a consequence, we confirmed that mean CV did not differ with n (e.g. 1.4 in $n = 4-27$ for females, Fig. S2a) but standard deviation of CV was larger with smaller n (e.g. 0.03 in $n = 26$ and 0.4 in $n = 4$ for females, Fig. S2b). Second, we sampled 4 year-colony data of annual mean body mass out of all available year-colony data and calculated CV; these were expected to be the most variable CVs, and repeated the process for all year-colony data combinations in each species including the comparison in Table 1 (year-data used: Table S3). For example, when five or 6 year-colony data were available, the number of combinations was 5 or 15, respectively. Comparing the 95% confidence interval of CVs among species (Fig. S3), the order of CVs in each species were similar as those when we calculated CVs from the raw data (i.e. CVs in Table 1). These two simulations indicated that CVs based on smaller sample sizes would be variable, but the difference in sample sizes did not strongly affect the result of inter-species comparison of CV in this study.

Body lipid stores

We calculated body lipid stores (body lipid mass ratio to body mass) in rhinoceros auklets during each breeding stage by dividing the mean body lipid mass by mean body mass (as described by Niizuma et al. 2002) and those reported for six other species of seabirds. The methods for measuring body lipid masses were Soxhlet extraction in ethyl ether from carcasses (three species, $n = 7$–30 for each species/stage, Taylor 1994; Niizuma et al. 2001b, 2002), folch reagent (chloroform and methanol) extraction from carcasses (three species, $n = 9$–32 for each species/stage, Jacobs et al. 2011), or body water content measurement by isotope dilution from living individuals (one species, $n = 67$ for combining two stages because of no significant stage-difference in body lipid stores, Chappell et al. 1993). The accuracy of measured lipid mass by the latter one method, estimating from living individuals indirectly, might be lower than by the former two methods, measuring from carcasses directly. The focus of our study, however, is not intra- or inter- individual variation but inter-species variation. Therefore, we believe that there is not large concern for comparing the average body lipid stores estimated by different methods in this study.

Results

Adult mass on Teuri Island

The mean of annual mean adult mass (± standard deviation SD) during incubation was 598 ± 15 g (range = 572–616 g, $n = 14$ years, Fig. 3a, Table S1) for males and 555 ± 12 g (range = 533–578 g, $n = 14$ years, Fig. 3b, Table S1) for females. CV across years was 2.5 for males and 2.2 for females and, but note these values are only for reference as we did not examine body mass throughout the incubation stage, furthermore, the sample size for each year was different.

The mean of annual mean adult mass (± standard deviation SD) during chick-rearing was 576 ± 8 g (range = 562–593 g, $n = 27$ years, Fig. 3a, Table S1) for males and 538 ± 8 g (range = 527–553 g, $n = 27$ years, Fig. 3b, Table S1) for females. CV across years was 1.4 for males and 1.4 for females (Table 1).

Combining 14 years of data when both data for the incubation and chick-rearing stage were available (Fig. 3, Table S1), females were 15 g heavier during the incubation than the chick-rearing stage whereas males were 20 g heavier (Table 2a). In 13 out of 14 years, adults of both sexes were heavier on average during the incubation than the chick-rearing stage (Fig. 3, Table S1).

In addition, we found a decrease in body mass in females (-0.26 ± 0.06 g day^{-1}) and males (-0.33 ± 0.04 g day^{-1}) during chick rearing at Teuri Island by LMMs (See Fig. S4 and Table S5 for summary of LMMs). This might suggest that adults become exhausted by chick rearing. Such seasonal

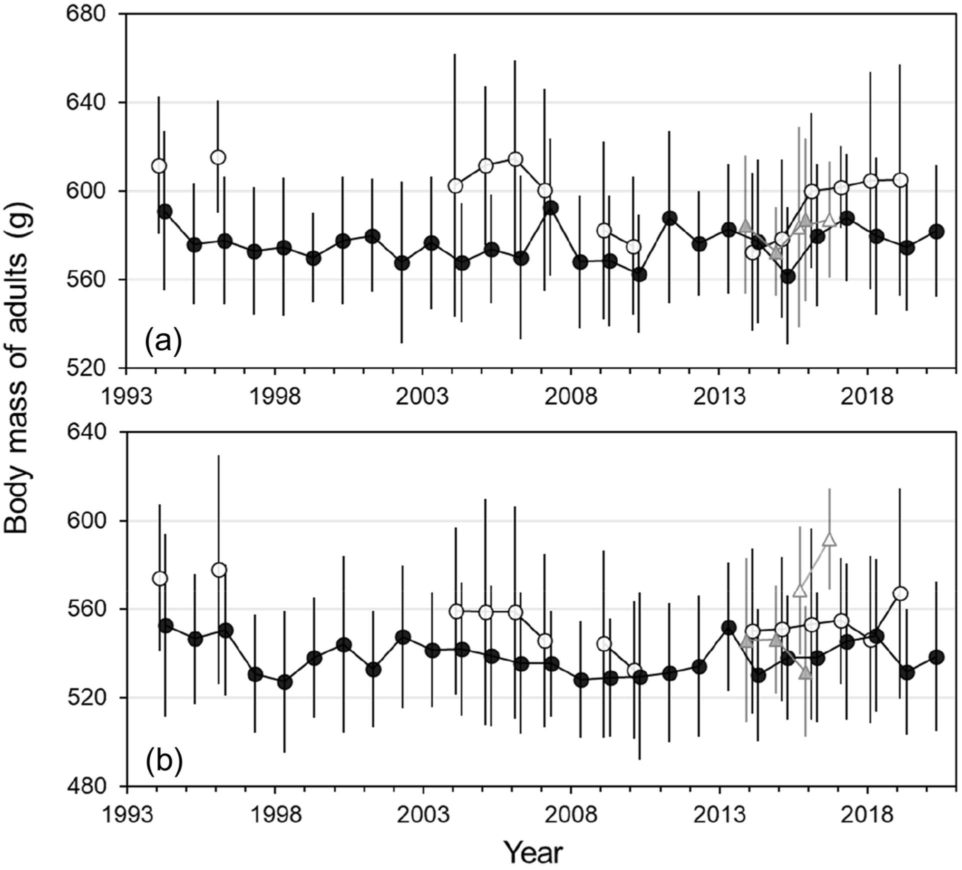

Fig. 3 Interannual change in body mass of rhinoceros auklets *Cerorhinca monocerata* breeding on Teuri Island (1994–2020) (**a** adult male; **b** adult female). Each plot and error bars indicate the mean and standard deviation on Teuri Island (black circles) and Daikoku Island (grey triangles). Solid symbols represent body mass during chick rearing and open symbols represent the incubation stage

Table 2 Comparison of adult body mass of rhinoceros auklets *Cerorhinca monocerata* between (a) breeding stages and (b) colonies

(a)		Incubation			Chick rearing			ANOVA		
Colony	Sex	Mean	SD	*n*	Mean	SD	*n*	*df*	*F*	*P*
Teuri Island	Female	553	40	261 (14)	539	32	696 (14)	1, 955	32.224	< 0.001
	Male	597	42	229 (14)	576	32	414 (14)	1, 641	48.806	< 0.001
Daikoku Island	Female	569	29	10 (1)	532	30	14 (1)	1, 22	9.0888	< 0.001
	Male	584	45	14 (1)	587	37	8 (1)	1, 20	0.0308	0.86
Total	Female	554	40	271 (15)	539	32	710 (15)	1, 979	36.872	< 0.001
	Male	596	42	243 (15)	577	32	422 (15)	1, 663	45.719	< 0.001

(b)		Teuri Island			Daikoku Island			ANOVA		
Breeding stage	Sex	Mean	SD	*n*	Mean	SD	*n*	*df*	*F*	*P*
Incubation	Female	553	40	261 (14)	582	28	24 (2)	1, 283	11.774	< 0.001
	Male	597	42	229 (14)	585	39	21 (2)	1, 248	1.6803	0.20
Chick rearing	Female	538	32	1520 (27)	541	30	41 (3)	1, 1557	0.2748	0.60
	Male	577	31	880 (27)	581	29	29 (3)	1, 907	0.5575	0.46

Mean and standard deviation (SD) of adult body mass are indicated with the number of individuals (n) and the number of sampling years in parentheses. Body mass was compared between breeding stages using individuals in years when we sampled both incubation and chick rearing (Fig. 3, Table S1). ANOVA statistics are also indicated

trends in adult body mass are of interest, but our aim is an inter-species comparison of the variability of annual mean body mass; therefore, we have indicated these results, but have not discussed them further.

Provisioning metrics on Teuri Island

Meal mass (Fig. 4a), fledging success (number of fledglings per nest with chicks) (Fig. 4b), chick growth rate (Fig. 4c) and fledgling mass (Fig. 4d) varied greatly between years (Watanuki et al. 2022). Inter-annual variability of meal mass (CV = 20.3, $n = 27$ years), fledging success (CV = 47.8, $n = 27$ years), chick growth rate (CV = 36.4, $n = 27$ years) and fledging mass (CV = 20.3, $n = 24$ years) were all much greater than those of body mass of females and males during the chick rearing and incubation stages. There were no significant correlations between adult mass and the four provisioning metrics in either females ($r = 0.03$–0.18, $P = 0.36$–0.88, $n = 24$–27 years) or males ($r = -0.18$–0.12, $P = 0.40$–0.73, $n = 24$–27 years).

Environmental variability index and provisioning metrics/adult mass

Testing correlation between the annual mean PDO and the four provisioning metrics or annual mean adult mass during chick rearing at Teuri Island, we confirmed the negative correlation for chick growth rate ($r = -0.48$, $P = 0.01$, $n = 27$, Fig. S7a), weak negative correlations for meal mass ($r = -0.34$, $P = 0.09$, $n = 27$, Fig. S7b) and fledging success ($r = -0.35$, $P = 0.08$, $n = 27$, Fig. S7c), while no correlation for fledgling mass ($r = 0.01$, $P = 0.96$, $n = 24$, Fig. S7d) and adult masses (females $r = 0.18$, $P = 0.36$, $n = 27$, Fig. S7e; males $r = -0.11$, $P = 0.58$, $n = 27$, Fig. S7f).

Inter-colony comparison of adult mass

Adult mass on Daikoku Island during chick-rearing did not differ significantly from that on Teuri Island in either females or males (Table 2b). In contrast, adult mass on Daikoku Island during incubation differs significantly from that on Teuri Island in females, but not in males (Table 2b). Despite the small sample size (3 years), the interannual variability shown by the CV of adult mass (1.4 for females and 1.3 for males) was similar to that on Teuri Island (1.4 for both females and males). On Daikoku Island, adult females were 41 g heavier during incubation than during chick-rearing (Table 2a, Table S1) and adult males were 4 g heavier, though the difference for males was not statistically significant (Table 2a, Table S1).

Species comparison of adult mass and provisioning metrics

The CV of rhinoceros auklet adult mass during the chick-rearing stage (1.4) was smaller than in 10 other species (1.7−7.5, Table 1), including four alcids (crested auklet *Aethia cristatella*, Atlantic puffin *Fratercula arctica*, thick-billed murre, common murre *U. aalge*), three procellariids (Wilson's storm-petrel *Oceanites oceanicus*, yellow-nosed albatross, short-tailed shearwater), cape gannet, black-legged kittiwake *Rissa tridactyla*, and Adélie penguin. In addition,

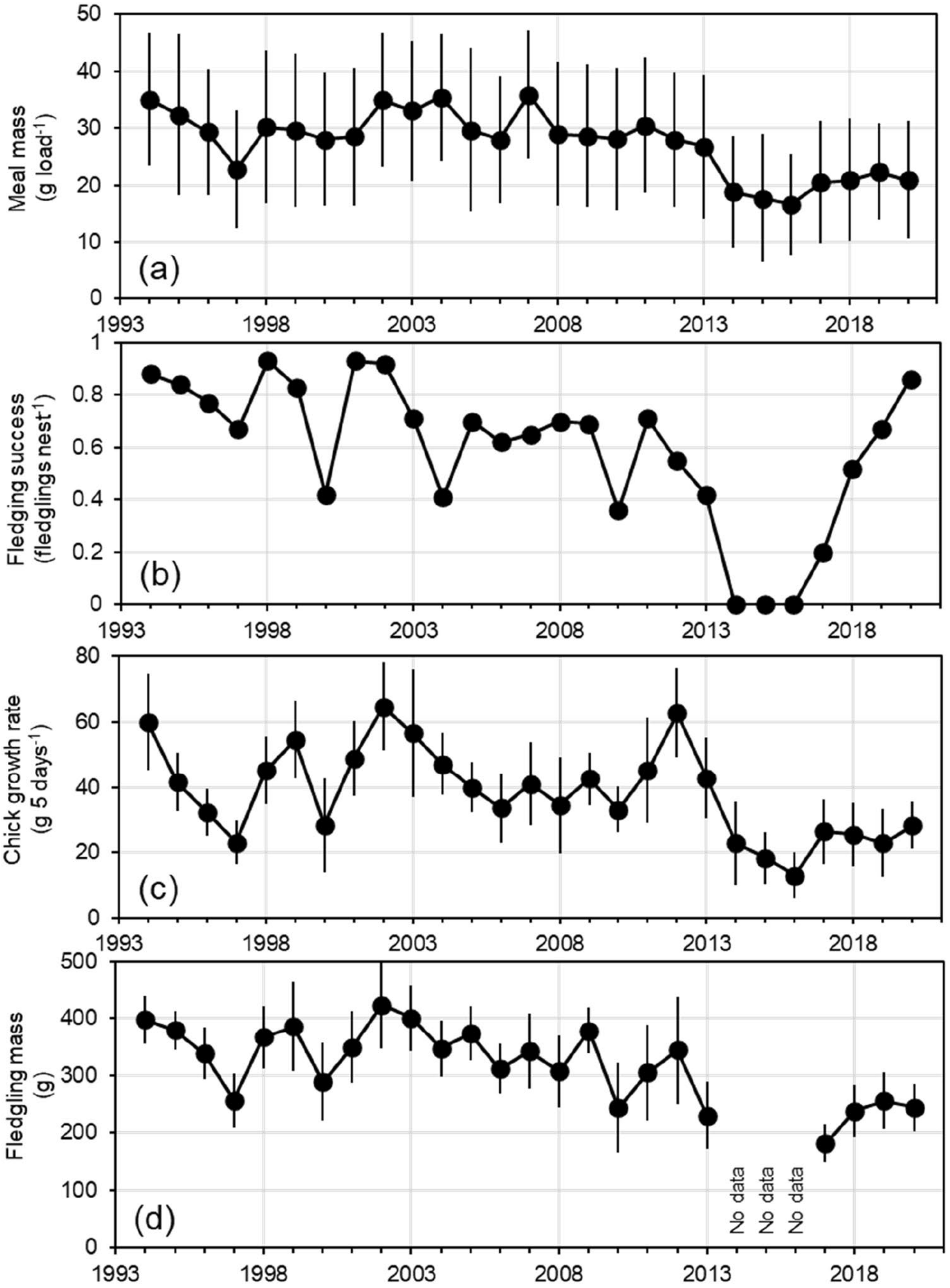

Fig. 4 Interannual changes in (**a**–**d**) provisioning metrics of rhinoceros auklets *Cerorhinca monocerata*. (**a**) meal mass; (**b**) fledging success (number of fledglings per nest with chicks); (**c**) chick growth rate; (**d**) fledgling mass. Data is from Watanuki et al. (2022). Each plot and error bars (indicated in (**a**), (**c**), and (**d**)) indicate means and standard deviation

we found that CVs for five alcids (1.4−3.8) and one procellariid (2.3−2.8) were relatively smaller than those of other seabirds (4.0−7.5). In contrast, the CV of provisioning metrics for rhinoceros auklet was the largest (chick growth rate, fledgling mass) or second largest (meal mass, fledging success) among these species (Table 1).

Body lipid stores

During the incubation stage, the body lipid stores of female rhinoceros auklets were 8.3% and those of males were 8.9%, and are comparable to those of incubating parents in other species (6.8–15.4%; Table 3). During the chick-rearing stage, however, the body lipid stores of females were 4.0% and those of males were 3.8%, and were smaller than those of chick-rearing parents in other species (5.7–9.5%; Table 3). The body lipid masses of incubating and chick-rearing male and female rhinoceros auklets at Teuri Island were 54 g in males ($n=8$, 611 g of mean body mass) and 48 g in females ($n=12$, 579 g) during the incubation stage, then 22 g in males ($n=11$, 578 g) and 22 g in females ($n=9$, 547 g) during the chick-rearing stage (Niizuma et al. 2002). The mean of annual mean body mass during chick rearing across 27 years (females: 538 ± 8 g, males: 576 ± 8 g)

Table 3 Seabird body lipid stores and body lipid mass ratio to body mass (%), during the incubating and chick-rearing stages

Family	Species	Body lipid stores (% body mass)		Method	References
		Incubation stage	Chick-rearing stage		
Alcidae	Rhinoceros auklet *Cerorhinca monocerata*	F 8.3 (12) M 8.9 (8)	F 4.0 (9) M 3.8 (11)	A	Niizuma et al. (2002)
	Little auk *Alle alle*	F 11.5 (14) M 10.1 (16)	F 6.6 (11) M 6.8 (16)	A	Taylor (1994)
	Thick-billed murre *Uria lomvia*	7.3 (32)	5.7 (9)	B	Jacobs et al. (2011)
Laridae	Black-legged kittiwake *Rissa tridactyla*	7.7 (12)	6.4 (19)	B	Jacobs et al. (2011)
Procellariidae	Northern fulmar *Fulmarus glacialis*	15.4 (20)	8.4 (11)	B	Jacobs et al. (2011)
	Leach's storm-petrel *Hydrobates leucorhous*	12.2 (7)	7.2 (12)	A	Niizuma et al. (2001b)
Spheniscidae	Adélie penguin *Pygoscelis adeliae*	F 6.8 [a] (37) M 9.5[a] (30)		C	Chappell et al. (1993)

Female (F) and male (M) values are shown for studies in which they were reported, with sample sizes in parentheses. The methods for measuring body lipid masses are Soxhlet extraction in ethyl ether from carcasses (A), folch reagent (chloroform and methanol) extraction from carcasses (B), or body water content measurement by isotope dilution from living individuals (C)

[a] Lipid mass is calculated as 0.904 (depot fat mass, g) according to Chappell et al. (1993). Body lipid stores did not differ significantly between two breeding stages in Adélie penguins, so the average of the breeding stages combined is shown

was comparable to the mean body mass used for Niizuma et al. (2002), indicated body lipid stores reported by Niizuma et al. (2002) were general in this species. Further, the lowest annual mean body mass of females was 527 g and that of males was 562 g (Fig. 3, Table S1), and were close to the body masses excluding body lipid masses during the chick-rearing stage (females 525 g; males 556 g; Niizuma et al. 2002).

Discussion

In this study, we examined the variation in the body mass of adult rhinoceros auklets between breeding stages and between years, using a 27-year data set at Teuri Island and a 4-year data set at Daikoku Island (as reference for confirming consistent trends across colonies). (1) Body mass during chick rearing was 15−20 g (2.7–3.4% of body mass) less than that during incubation (Fig. 3; Table 2). (2) We found no correlation between provisioning metrics and body mass. (3) For Teuri Island birds, the annual variation in the PDO, indexed as anchovy availability, was negatively correlated with the provisioning metrics in each year, except for fledgling mass, but not with adult mass during chick rearing (Fig. S7). (4) Interannual variability in body mass during chick rearing was small (Fig. 3; Table 1) but in provisioning metrics, it was large (Fig. 4). (5) Comparing the interannual variability (CV) in body mass during chick rearing among 11 seabird species including five alcids, the CVs were the smallest for the rhinoceros auklet (Table 1). (6) We also found the body lipid stores of rhinoceros auklets was smaller than in six other species (Table 3). Hereafter, we discuss about body mass variation in rhinoceros auklets briefly (results 1−4 above), then about main hypotheses of this study given inter-species comparisons of body mass variability and body lipid stores (results 5−6 above).

Body mass and provisioning metrics of rhinoceros auklets

Combining data from Teuri Island and Daikoku Island, the mean body mass of females was 15 g heavier during incubation than during chick rearing and for males, it was 20 g (Table 2). Such mass loss during the chick rearing stage was previously described from one year's data on Teuri Island (Niizuma et al. 2002), and we suggest that it is general across years and probably between colonies with contrasting marine environments (but there was no difference among males on Daikoku Island; Table 2). The reduction in parental body mass from the incubation to the chick-rearing stages is hypothesized to allow them to fly more economically during extensive foraging journeys while bringing heavy meals for their chicks (Nordberg 1981; Moreno 1989; Jones 1994); this is known as "adaptive mass loss". Rhinoceros auklet parents can reduce their flight costs by 9–10% by losing 30 g of their body mass (Niizuma et al. 2002), given 15−20 g mass loss on average, they would save 5−7% of their flight costs. We observed a reduction in body mass between the incubation and chick rearing stages in 13 year-colony out of 15 for females and 14 out of 15 for males, but the extents varied among year-colony (mean ± SD (min−max): 18 ± 11 (− 4−37) g for females, 21 ± 15 (− 5−45) g for males, *n* = 15 year-colony, Table S1). Such year-colony variation has been reported also in thick-billed murres (Gaston and Hipfner 2006b) and little auks *Alle alle* (combined results from Taylor 1994; Wojczulanis-Jakubas et al. 2012, 2014, 2015); this might reflect nutritional stress resulting from the difference in prey availability between year-colonies (Gaston and Hipfner 2006b). The main objective of our study was an inter-specific comparison of the variability in annual mean body mass, therefore, we do not discuss the relationship between the extent of mass loss and environment in rhinoceros auklets. In addition, individual variation in body mass through the breeding seasons and between years provides further material for testing the adaptive mass hypothesis.

The PDO was negatively correlated with the provisioning metrics except for fledgling mass, but not with adult mass during chick rearing (Fig. S7). The stock size of Japanese anchovy, one of the most profitable prey species for rhinoceros auklets, tends to increase in negative PDO phase (i.e. warm years in North Western Pacific, 1998−2013) (Takasuka et al. 2008, but see Kuroda et al. 2020). Indeed, on Teuri Island, the mass proportion of Japanese anchovy in the diet for rhinoceros auklet chicks was high during the negative PDO phase (84 ± 10%, mean ± standard deviation, in 1998−2013), but medium or almost zero during the positive PDO phase (53 ± 31% in 1994−1997, 2 ± 3% in 2014−2020); the provisioning metrics showed the decadal variation roughly coinciding with the proportion of anchovy in the diet (Watanuki et al. 2022). Thus, the negative correlation between the PDO and the provisioning metrics would be occurred via the interannual change in availability of Japanese anchovy. The complete breeding failures in 2014–2016 (Fig. 4b) would be due to abrupt decrease in anchovy availability (Watanuki et al. 2022), although fledging success have recovered somewhat since 2017, probably due to feeding the alternative prey species more, sand lances *Ammodytes* spp. or greenlings *Pleurogrammus azonus*. Though we did not analyze in this study, as well as the environmental variability index across the North Pacific (i.e. the PDO), the interannual variation in local ocean current expansion or air temperature during breeding season also could affect the provisioning metrics via change of availability of Japanese anchovy or breeding phenology (Watanuki et al. 2009). The results from Teuri Island so far suggest that parents of rhinoceros auklets vary the investment to their chicks largely with the interannual environment variation as well as the previous studies in California, Canada (Hedd et al. 2006; Thayer and Sydeman 2007). The large interannual variability shown by the CV of the provisioning metrics (20.3–47.8) at Teuri Island found in this study supports this. The CV of meal mass at Daikoku Island (20.4) was also large (22.0 g in 2014, 21.5 g in 2015, 18.8 g in 2016, and 29.7 g in 2017; Okado et al. 2020, 2021). Despite the large interannual variability in provisioning metrics, we found that interannual variability in adult body mass, as indicated by the CV at Teuri Island (1.4 for females and males) and at Daikoku Island (1.4 for females and 1.3 for males), was small and there was no interannual correlation between body mass and either the PDO or provisioning metrics. This indicates that rhinoceros auklets maintain their body mass within a certain range during chick rearing even in a variable environment.

Inter-species comparison

In comparing differences in interannual variability of adult mass between species, it is important to note that we sampled adults raising chicks whereas some other studies sampled both breeders and non-breeders (Table 1). Because of the small number of studies that have examined interannual variation in body mass, we were forced to include studies that did not exclude non-breeding individuals. In both Atlantic puffin and least auklet *Aethia pusilla*, the body mass of non-breeders is relatively smaller than that of breeders (Harris 1979; Jones 1994). Additionally, some studies have shown that the proportion of non-breeders increases in years with poor environmental conditions (Cubaynes et al. 2011; Jean-Gagnon et al. 2017). We were unable to rule out the possibility that the interannual variability (CV) in body mass during the chick-rearing stage could be large in those studies that included non-breeders. However, the CV of rhinoceros auklet body mass (1.4) in our study is lower than that of five other studies where only breeders were sampled (Table 1). Therefore, we are still confident that the interannual variability in body mass of chick-rearing rhinoceros auklets is the smallest among 11 seabird species (Table 1).

The interannual variability in rhinoceros auklet body mass during chick rearing was the smallest among seabirds including four alcids (Table 1). The minimum level of body lipid stores in chick-rearing rhinoceros auklets, which is only 40–70% of stores carried by five other seabirds (Table 3), may force them to maintain body mass within a narrow range. The wing loading of adult rhinoceros auklets is 12.7 kg m^{-2} for 560 g body mass on average (Spear and Ainley 1997, mean body mass of chick-rearing adult males and females on Teuri Island: 557 g), it is within 95% confidence interval of the predicted value based on the body mass to wing load relationship in alcids (Fig. 1). However, rhinoceros auklets, confined to delivering at most one meal per parent daily, carry the unusually large meals relative to their body size (the heaviest meals among alcids despite being medium-sized species, Gaston and Jones 1998), therefore, reducing body lipid stores and saving flight costs may be essential for them to rear chicks. While, they are also at risk of reduced survival if they lower their body lipid stores further. It is well known that seabird parents use up their body lipids first, then consume body proteins once their body lipid stores approach a minimum level during starvation (Cherel et al. 1988) and are thus likely to abandon breeding to increase their possibility of surviving (Groscolas et al. 2000, 2008). Chick-rearing rhinoceros auklets, therefore, may be forced to maintain a body mass as close as possible to the minimum level for survival. Therefore, they may not have the flexibility to adjust their body mass, even when environment changes between years.

This inflexibility regarding body mass regulation may explain the rhinoceros auklet's large interannual variation in provisioning metrics (i.e. investment in their chicks, Table 1, Fig. 4). Seabird parents are long lived with multiple opportunities to breed, thus may prioritize their own survival over reproduction so as to maximize their life-time fitness (Clutton-Brock 1991; Stearns 1992). Therefore, they might choose to abandon current reproduction if their body mass (body lipid stores) falls below a threshold that reduces their survival under poor environment (Groscolas et al. 2000; 2008). Such a threshold, related to parental decisions on reproduction, may differ between species or breeding stage (Monaghan et al. 1992; Gaston and Hipfner 2006a). Although we could not confirm the actual threshold at which rhinoceros auklets abandon breeding in this study, we found that they have only limited body lipid stores during chick rearing and, surprisingly, they were expected to show little body lipid stores in some years (e.g. 1998, 2008, and 2009 for females; 2010 and 2015 for males; Fig. 3; Table S1). These results suggest that body mass is maintained close to the theoretical threshold which may reduce survival during chick rearing. Adult rhinoceros auklets are unable to reduce their body mass during chick rearing even under conditions of changing environment, instead they change their investment in their chicks as shown provisioning metrics (Table 1). Such flexibility in provisioning metrics could allow parents which cannot compromise their own energetic requirements to buffer suboptimal foraging condition but it would result relatively large interannual variability in provisioning metrics, including total breeding failure in some years (2014–2016; Fig. 4b).

Conclusion

To conclude, this study demonstrates that chick-rearing rhinoceros auklets maintain their body mass within a narrow range. Our inter-species comparison highlights the importance of flight costs in relation to wing loading and meal mass in the regulation of body lipid stores, which may constrain the allocation of resources between parents and offspring under conditions of high interannual environmental variability.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-023-04271-8.

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Author contribution All authors contributed to the study conception and design. Analysis was performed by JO with input from YW. Material preparation and data collection were performed by YW and JO. The first draft of the manuscript was written by JO and revised by JO and YW. All authors read and approved the final manuscript.

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Data availability The results of our analyses are presented as the main tables and figures. We have also included the data for mean provisioning metrics or body mass for each species used in this study as supplementary information. The raw data for rhinoceros auklets will be made available upon request.

Declarations

Conflict of interest The authors declare no conflicts of interest associated with this manuscript.

Ethical approval The fieldwork was carried out under permits, including ethical issues, from the Ministry of the Environment (591, 248, 88, 040315003, 050318001, 060331001, 070328001, 100303001, 110309001, 120209001, 1302151, 1403031, 1503165, 1603291, 1703211, 1802231, 1902122, 2003043, 1405141, 1504221, 1605123, 1704282) and the Agency for Cultural Affairs (3353, 16-4-1810, 20-4-85, 22-4-2126, 23-4-1990, 24-4-2133, 25-4-2033, 26-4-2188, 27-4-1928, 29-4-18, 29-4-1838, Gan-4-1920), and Animal Ethics Committee of Hokkaido University (09-0021, 16-0054).

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