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ORIGINAL PAPER

Sex allocation in a monomorphic seabird with a single-egg clutch: test of the environment, mate quality, and female condition hypotheses

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Abstract Sex allocation theory posits that mothers should preferentially invest in sons when environmental conditions are favorable for breeding, their mates are of high quality, or they are in good body condition. We tested these three hypotheses in rhinoceros auklets (*Cerorhinca monocerata*), monomorphic seabirds that lay a single-egg clutch, in 2 years that differed in environmental conditions for breeding. Results supported the environment and mate quality hypotheses, but these effects were interactive: offspring sex was independent of paternal traits in the poor year for breeding, while females mated to larger and more ornamented males reared more sons in the better year. Conversely, offspring sex was unrelated to female condition, as indexed by hatching date. We propose that good rearing conditions enable females to rear sons possessing the desirable phenotypic attributes of their mates. Results also supported two critical assumptions of sex allocation theory: (1) dimorphism in offspring condition at independence: daughters fledged with higher baseline levels of corticosterone than sons and (2) differential costs of rearing sons versus daughters: mothers rearing sons when environmental conditions were poor completed parental care in poorer condition than mothers rearing daughters in the same year and mothers rearing either sex when conditions were better. These novel results may help to explain the disparate results of previous studies of avian sex allocation.

Keywords Body condition · Reproductive investment · Resource holding potential · Sex ratio · Trivers–Willard hypothesis · Mate quality

Introduction

Greater variance in reproductive success of males compared to females sets up the possibility for selection on mothers to differentially allocate investment in male versus female offspring in a condition-dependent manner (Trivers and Willard 1973). Such differential allocation is predicted to result in larger or otherwise higher-quality sons, as the relative fitness payoff of producing high-quality sons exceeds that of high-quality daughters, an ultimate basis for fledgling sexual dimorphism. Underlying the theory of sex allocation (Charnov 1982) are two assumptions: that the costs of rearing larger, high-quality sons exceed those of rearing daughters (Clutton-Brock et al. 1981) and that there is sexual dimorphism in the size or condition of the offspring at the end of the parental care period (Trivers and Willard 1973; Benito and Gonzalez-Solis 2007). Factors hypothesized to influence sex allocation decisions include environmental conditions (Charnov 1982, 1986), quality of mates (Fawcett et al. 2007), and individual

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female condition (Trivers and Willard 1973; Charnov 1982; Schwanz et al. 2006).

When mothers experience good environmental conditions (Suorsa et al. 2003) or are in good condition (Whittingham et al. 2002; Sheldon and West 2004; Dowling and Mulder 2006), they are expected to produce more offspring of the more expensive sex, usually sons, because these will mature to large body size and good condition. Mothers also are expected to bias their reproductive efforts towards sons if mated to males of high genotypic quality, as their sons will inherit the qualities of their fathers (Ellegren et al. 1996; Saino et al. 2002; Gwinner and Schwabl 2005). Survival prospects (Svensson and Nilsson 1996), age (Long and Pischedda 2005; Dowling and Mulder 2006), ornamentation (Ellegren et al. 1996), and size or resource holding potential (Kölliker et al. 1999) are among the phenotypic qualities of their mates that might cause mothers to bias their reproductive efforts towards sons. Size, condition, and other phenotypic traits could asymmetrically affect males when they are subject to intersexual and intrasexual selection to obtain mates, hold territories, or queue for resources.

Trivers and Willard (1973) developed their theory of sex allocation with single-offspring red deer (*Cervus elaphus*) in mind and considered allocation by mothers affecting the sex ratio of offspring at independence (see also Frank 1990). Yet most previous avian research has measured individual sex allocation decisions in species that lay multiple-egg clutches, where the bias is numerically less than 100% (references in Ewen et al. 2004; but see Komdeur et al. 1997; Blanchard et al. 2007). Moreover, much of the literature has shifted towards measuring primary sex ratio (e.g., Ewen et al. 2004; Rosivall 2008), which is only one small component of sex allocation as envisioned by Trivers and Willard (1973). Thus, the avian literature is depauperate on the importance of sex allocation in the single-offspring life history strategy, in which the sex allocation decision is likely to have particularly stark consequences for offspring quality and sex ratio at independence.

We measured sex ratios just prior to fledging in the rhinoceros auklet *Cerorhinca monocerata*, a long-lived, colonial, burrow-nesting seabird that lays a single-egg clutch and exhibits slight sexual size dimorphism (males are on average 10% heavier than females and have larger horn ornaments—a bill plate modification which protrudes above the top of the culmen only during the breeding season, before being shed, giving the species its name (Gaston and Dechesne 1996). We also measured body mass and size and the size of the horn ornament, as well as baseline and response (to standardized handling and restraint for 30 min) corticosterone in mothers and fathers, in addition to body size and mass and baseline corticosterone in offspring. Corticosterone has proven an effective means to index nutritional condition in seabirds (Kitaysky et al. 2001, 2005). We carried out the study in 2 years, one (2003) a mild El Niño year featuring warm overwinter sea surface temperatures (DFO 2004) and weak spring marine primary production (Wolf et al. 2008) that for rhinoceros auklets resulted in late laying (median 7–11 May) and poor hatching success (just 46% of early-laying pairs hatched eggs), the other (2004) a year of cool overwinter sea surface temperatures (DFO 2005) and stronger spring marine primary production (Wolf et al. 2008) that resulted in earlier laying (median 2–6 May) and higher hatching success (93% among early layers). Of note, almost all chicks that hatched survived to fledge in the 2 years (91% and 93%; Hipfner et al. 2008).

In rhinoceros auklets, variance in reproductive success is likely greater in males than females because of the importance of male size in their ability of acquire and maintain burrow sites (Jones and Hunter 1999 found this in a closely related species). Thus, following Trivers and Willard (1973) and more recent syntheses of sex allocation theory (i.e., Charnov 1982; Frank 1990; Fawcett et al. 2007), we predict that (1) environment hypothesis: female rhinoceros auklets will fledge proportionately more sons than daughters in 2004, the more favorable year, and fledge proportionately more daughters than sons, in 2003, the less favorable year; (2) mate quality hypothesis: mothers mated to larger and more ornamented males will preferentially produce sons; and (3) female condition hypothesis: early-laying females will preferentially fledge sons, whereas late-laying females will fledge daughters. Laying date is a useful proxy for the phenotypic condition of female rhinoceros auklets because in other Alcidae earlier-laying females are older, more experienced, more successful (DeForest and Gaston 1996), and in better body condition (Gaston and Hipfner 2006) than later-laying females. Experiments indicate that the seasonal decline in breeding success for rhinoceros auklets at Triangle Island is causally related to date and independent of the other attributes of early- and late-laying pairs (Hipfner et al. 2008). In such situations, we expect phenotypically high-quality females to lay early (Verhulst and Nilsson 2008). We also test two assumptions of sex allocation theory: (1) that there will be sexual dimorphism among offspring at the end of the parental care period and (2) that the costs for both parents of rearing sons exceed those of rearing daughters.

Materials and methods

Field methods

Our study site was Triangle Island, British Columbia, Canada (50° 52' N, 129° 05' W). Burrows on study plots (two adjacent plots in 2003, one plot in 2004) were monitored for phenology, breeding success, and chick growth between April and August, as described in Hipfner et al. (2004). After 45 days of age, chicks were captured from burrows in late afternoon and immediately had 100–200 μL of blood drawn from the alar vein with a 1-cm^3 syringe and 27-g needle, followed by weighing and measuring of tarsus and wing chord. Blood samples were promptly centrifuged at 8,000 rpm for 8 min, and plasma were separated from red blood cells for baseline corticosterone analysis. Red blood cells were stored in 95% ethanol for genetic sexing, and both red blood cells and plasma were stored frozen in the field. Soon after sampling chicks, we captured parents from their burrows after they had made their provisioning deliveries (rhinoceros auklets are nocturnal provisioners). Captured adults were blood-sampled for genetic sexing and corticosterone assays immediately and 30 min after capture (to measure adrenocortical response to capture and restraint, hereafter "response corticosterone"), banded, and measured (mass, tarsus, wing, culmen, bill depth, horn height), then returned to their burrows. We did not detect any abandonment or change in provisioning habits as a consequence of capture.

Laboratory analyses

After returning from the field, we shipped plasma samples to the radioimmunoassay laboratory at the University of Alaska Fairbanks and stored them at −80°C. Following Wingfield and Farner (1975), we measured concentrations of corticosterone in 20-μL plasma. Steroids were extracted in 4 mL of dichloromethane, and concentrations were measured in duplicate. Recovery values ranged from 87% to 98% (average 92%) following extraction, and assayed concentrations were evaluated by comparison with a standard curve and adjusted as appropriate. All samples were analyzed in a single assay; intra-assay coefficient of variation was 2.3% and assay sensitivity was 7.9 pg per tube.

Genetic samples were stored at −20°C at Simon Fraser University. All samples were extracted twice using an ammonium acetate extraction with an ethanol precipitation. DNA was quantitated and diluted if needed. We amplified the sex-linked CHD gene using the 2550F–2718R primer pair and conducted polymerase chain reaction (PCR) in 15-μL reactions as in Dawson et al. (2001). PCR products were viewed on 3% agarose gels stained with ethidium bromide.

Statistical analysis

We assessed chick sex ratios for each year of the study using a binomial test evaluating observed offspring sex ratios against a null expectation of 0.5.

We use AIC$_c$ model selection to compare among the three hypotheses for sex allocation. This approach allows us to determine which combination of factors might be working together to influence offspring sex allocation. Using multimodel inference, we calculate AIC$_c$ weights to determine the relative importance of each parameter. To test the three hypotheses, we selected seven logistic regression models including a variety of parameters (year, hatch date (=mother condition), year×hatch date interaction, father quality principal component (see below), father quality× year interaction) for predicting offspring sex, including a global model containing all parameters and interaction terms of interest and a null model. Hatch date was used rather than lay date because we had better information for hatch date, and there is little variance in incubation time. Father "quality" was indexed using a principal component derived from skeletal measurements (culmen, bill depth, tarsus) and horn height above the bill. This gives an overall measure of size and ornamentation. Bill plate and plumage ornaments and body size have been shown to function in mate choice by females in other species of Alcidae (Jones and Hunter 1993, 1999; Jones et al. 2000). The first principal component explained 49% of the variance and had roughly equal and positive loadings (range 0.45–0.56) for all measures included, indicating it is a good measure of overall size. Of note, there was no assortative mating by size and ornamentation scores within pairs (r^2=0.04).

We had 11 missing values for father "quality" because we did not capture all chicks' fathers (five nests in 2003 and six nests in 2004). Therefore, we generated a second dataset with mean values (for principal component scores mean is zero by definition) to substitute for missing values in order to validate conservatively the results detected with our smaller dataset. All models were fitted to both datasets in SAS v.6 using proc genmod with binomial error distribution and link logit function, and we calculated AIC$_c$ values for each model in separate analyses for each dataset. We then ranked model parameters by summed AIC$_c$ weights and calculated weighted parameter estimates by multimodel inference for each dataset (Burnham and Anderson 2002).

To test the assumption that sons fledge larger and in better condition than daughters, we used AIC$_c$ selection of linear models comparing the effect of sex versus a null model for fledging mass, wing length, and plasma baseline corticosterone. To test the assumption that it is costlier for parents to rear sons than daughters, we indexed parental condition from a principal components score of mass–tarsus body condition, baseline corticosterone, and response corticosterone, calculated separately for mothers (n=23) and fathers (n=26). Principal component 1 explained 42% of the variation for mothers and 44% of the variance for fathers and had roughly equal loadings that were positive

Table 1 $\mathrm{AIC_c}$ values for models ranked better than the null model of the dataset with missing values for father quality (n=25) and dataset with mean values for missing values (n=36)

Model	K	Number	Error df	LgLik	$\Delta\mathrm{AIC_c}$	$\mathrm{AIC_c}w$	Evidence ratio
Father	3	25	22	−15.4395	0.0000	0.2920	1.0
Year	3	25	22	−15.7324	0.5858	0.2178	1.3
Null	2	25	23	−17.1482	0.8200	0.1938	1.5
Year, father, year×father	5	36	31	−19.9613	0.0000	0.3171	1.0
Father	3	36	33	−22.6754	0.1782	0.2901	1.1
Null	2	36	34	−24.4510	1.3430	0.1620	2.0

K is the number of model parameters; Number is the number of observations; error degrees of freedom is calculated from Number and K; log likelihoods (LgLik) are from logistic regression analysis predicting offspring sex. $\Delta\mathrm{AIC_c}$ values, weights, and evidence ratios are calculated from Burnham and Anderson (2002).

for corticosterone measures and negative for body condition, so that, for both mothers and fathers, high values of condition principal component (PC) correspond to poor overall condition. We used $\mathrm{AIC_c}$ model selection to compare the analysis of variance model year, offspring sex, the saturated model including the interaction term, and a null model for each of the mother and father condition.

Results

Offspring sex ratios at independence did not differ from equality in 2003, the year of later and less successful breeding (ratio=11f:12m, binomial test P=0.86). In contrast, even with a modest sample size, we detected significant overproduction of males in the better year, 2004 (ratio=4f:12m, P=0.04).

Sex allocation: tests of multiple hypotheses

The logistic models containing year×father parameters in the truncated dataset (due to missing values) had convergence problems, likely due to few female offspring in 2004. Therefore, we excluded this interaction term from all analyses of this dataset. The $\mathrm{AIC_c}$ analysis of the truncated dataset selected father as the best-fit model (Table 1) and year as second. The third ranked model was the null model, so other models cannot be considered to have received substantial support. The conservative analysis of the dataset with mean values substituted for missing values similarly selected year, father, year×father as the best-fit model (Table 1) and father as second. Again, the third ranked model was the null model, so other models received relatively little support.

The $\mathrm{AIC_c}$ weights of parameters in both analyses selected father as the most important parameter and year second (Table 2). All the weighted parameter estimates substantially bound zero, so we cannot make inferences from this component of the analysis. Furthermore, plots of father PC score by year and offspring sex show no overlap in the PC scores of fathers of daughters and sons in 2004 but near total overlap in 2003 (Fig. 1). Fathers of daughters constituted the smallest males measured in 2004. These data are strongly suggestive of interactive effects of year (environmental conditions) and father quality and little or no influence of hatch date (an indicator of mother condition).

Sex allocation: tests of assumptions

Sons and daughters differed by less than 2% in fledging mass (overall average 262 g±7 SE, n=36, null model K=1, $\mathrm{AIC_c}w$=0.7408; chick sex K=2, $\mathrm{AIC_c}w$=0.2592) or wing

Table 2 $\mathrm{AIC_c}$ weights and weighted parameter estimates and 1 SE for all parameters in models from the $\mathrm{AIC_c}$ analysis

	n=25		n=36	
Parameter	Summed $\mathrm{AIC_c}w$	Estimate$w$±1 SEw	Summed $\mathrm{AIC_c}w$	Estimate$w$±1 SEw
Intercept		3.1178±4.9989		2.5765±4.3154
Father	0.4397	0.2956±0.2522	0.6389	2.0953±2.4893
Year	0.3851	−0.9361±1.2577	0.4770	−1.8456±2.5048
Year×father			0.3488	−1.8291±2.1005
Date	0.1593	−0.0150±0.0177	0.1185	−0.0114±0.0154
Year×date	0.0301	0.0025±0.0053	0.0476	0.0084±0.0116

The truncated dataset has n=25; the dataset with mean values for missing values has n=36. Father quality is ranked most important among variables included in the model set

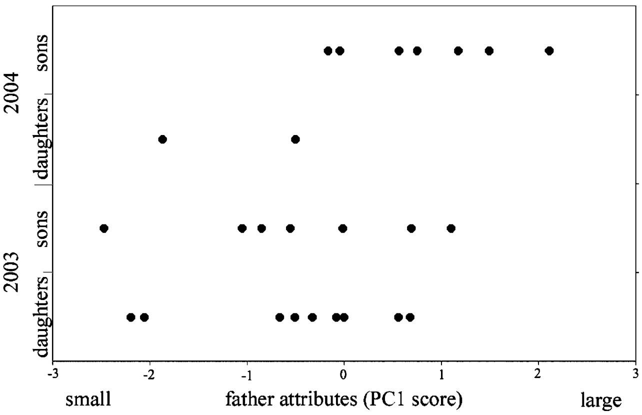

Fig. 1 PC score for father quality, for fathers of sons versus daughters in 2003, a year of poor environmental conditions, and 2004, a year of good conditions. The PC weighted equally and positively on measures of father skeletal size and horn ornamentation

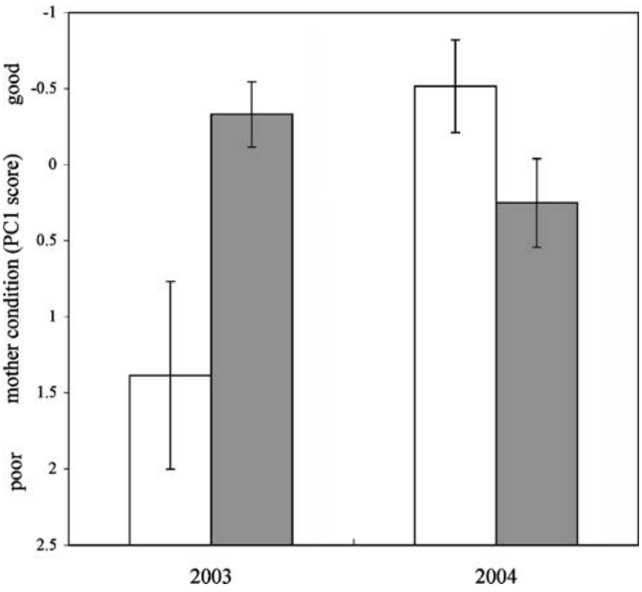

Fig. 2 Mother condition (±95% CI), indexed by a PC of mass–tarsus, baseline corticosterone, and response corticosterone, of mothers rearing sons (*white bars*) versus daughters (*gray bars*) in 2003, a poor year, and 2004, a good year. The axis is reversed because lower PC scores correspond to higher condition (low corticosterone and higher mass–tarsus)

chord (overall average 150 mm±1, $n=36$, null model $K=1$, $\mathrm{AIC_c}w=0.7088$; chick sex $K=2$, $\mathrm{AIC_c}w=0.2912$) measurements. However, daughters had higher baseline corticosterone (9.709 ng/mL±2.110) than sons (4.883 ng/mL±0.664; $n=36$, chick sex $K=2$, $\mathrm{AIC_c}w=0.8881$, null model $K=1$, $\mathrm{AIC_c}w=0.1119$).

Measurements and corticosterone values for parents are summarized in Table 3. Different models were selected for best fit of mother and father condition. For father condition, the model including only year was the best fit ($K=3$, $n=22$, $\mathrm{AIC_c}w=0.6228$) and the only model better than the null ($K=2$, $n=22$, $\mathrm{AIC_c}w=0.2090$). By contrast, the best model for mother condition was the saturated model including year, offspring sex, and the interaction term ($K=5$, $n=23$, $\mathrm{AIC_c}w=0.6019$) and was the only model better than the null ($K=2$, $n=23$, $\mathrm{AIC_c}w=0.2225$). Mother condition at the end of chick rearing was dependent on an interaction between year and offspring sex (Fig. 2). Mothers rearing sons in 2003 were in poorer condition than those rearing daughters in 2003 or rearing any sex in 2004.

Discussion

Female rhinoceros auklets differentially allocated to sons and daughters: we found support for both the environment and father quality hypotheses. Unexpectedly, however, the two worked interactively. In 2003, females mated to large and small males produced sons and daughters in equal proportions; environmental conditions might not have been sufficiently poor to create strong incentive for females to allocate towards daughters. In contrast, in 2004, when environmental conditions were better, the sex ratio was, as predicted, highly skewed towards sons and very dramatically among females mated to large and well-ornamented males; only females mated to the smallest males in the population reared daughters.

Early-rearing conditions can have lasting effects on adult phenotype (Metcalfe and Monaghan 2001), so good rearing conditions may be important for ensuring that sons achieve the high phenotypic quality of their fathers. The interactive effects of father quality and yearly conditions likely arise from the need for good environmental conditions during the rearing period to take advantage of a father's good genes and rear sons that share his desirable phenotypic traits (Sheldon et al. 1997). Our principal component for male quality encompassed both size and ornamentation and thus is likely to incorporate important factors determining a male's ability to attract mates and acquire and hold burrows

Table 3 Mean (SD) of parental measurements included in the principal components analysis for parental quality

	Number	Mass (g)	Tarsus (mm)	Horn (mm)	Plasma corticosterone	
					Baseline (ng/mL)	30 min (ng/mL)
Fathers	26	523 (23)	31.1 (1.1)	26.0 (1.7)	11.005 (12.116)	55.315 (20.341)
Mothers	23	487 (15)	30.6 (0.9)	22.6 (1.8)	9.131 (7.030)	51.953 (13.498)

(Jones and Hunter 1999); defense of burrows can result in physical fights in rhinoceros auklets (Gaston and Dechesne 1996). In contrast, we found no support for the female condition hypothesis: earlier-laying females were not more likely to produce sons.

Brood sex ratio is an all-or-nothing proposition in species that lay a single-egg clutch, like rhinoceros auklets, and this may actually present stronger incentive for females to alter investment in different sexes compared to species that lay multi-egg clutches, which can partially bias sex ratio. Extreme sex ratio variation has previously been noted in a single-egg clutch species (Komdeur et al. 1997) but, to the best of our knowledge, our dataset presents the first opportunity to test among three competing hypotheses for differential sex allocation in an avian species rearing only one offspring per breeding effort. We suggest that it is because of our focus on a species with a single-egg clutch that we were able to detect these effects even with modest sample sizes.

We also found that two underlying assumptions of sex allocation theory hold in rhinoceros auklets, sexual dimorphism in fledging condition and differential costs to parents of rearing sons and daughters. Sexual dimorphism in fledging condition remains unobserved in many studies (e.g., Saino et al. 2002) or is dependent on hatching order (e.g., McDonald et al. 2005) in species with extreme adult sexual dimorphism. Nutritional bias has been proposed as a form of differential sex allocation (Magrath et al. 2004). Rhinoceros auklet chicks increase baseline corticosterone when experiencing food shortage, and there is no sex effect on corticosterone response (Sears and Kitaysky unpublished data); thus, higher baseline corticosterone in daughters could indicate that parents feed daughters less or more intermittently than sons, as in common murres (*Uria aalge*; Cameron-MacMillan et al. 2007). The lack of difference in mass confuses this result but could indicate that sons have higher maintenance costs. However, because few other studies have considered physiological measures of offspring condition (Saino et al. 2002), our result of higher baseline corticosterone in daughters, despite a lack of difference in fledging mass and size, is novel. In other marine birds, high corticosterone during development has been shown to impact cognitive function later in adult life (Kitaysky et al. 2006); thus, elevated corticosterone in daughters could present a serious impediment later in life.

The assumption of differential costs of raising sons and daughters has been validated previously (Clutton-Brock et al. 1981; Magrath et al. 2007). However, in our study, mothers that reared sons completed chick rearing in poorer condition than mothers that reared daughters in 2003, the El Niño year featuring delayed laying and poor hatching success, but there was little difference in 2004, the more favorable year of earlier laying and much higher hatching success. That interaction suggests that females might pay a particularly high price to rear sons in poor years. Moreover, the difference in baseline corticosterone of sons and daughters corroborates the evidence that mothers may invest more in sons. Interestingly, year rather than offspring sex was the primary predictor of father condition, suggesting that fathers do not markedly adjust effort according to the sex of their offspring, which is in contrast to findings in a previous study of paternal effort in the Alcidae (Cameron-MacMillan et al. 2007). This important result is suggestive of stronger incentives for mothers than fathers to alter offspring sex when environmental conditions are poor.

We measured fledging sex ratio in our study. Original sex allocation hypotheses focused on resource investment in male versus female offspring and the resulting sex ratio at the end of parental care (Trivers and Willard 1973; Frank 1990). Much recent literature has focused on primary sex ratio adjustment, but there is cumulatively little evidence for adjustment of primary sex ratio in birds (Ewen et al. 2004). However, sex ratios might be adjusted later in the breeding episode (Almond and Edlund 2007) via differential hatching success due to allocation of (Badyaev et al. 2006) and sensitivity to (Love et al. 2005) hormones or other maternal contributions to eggs. In our species, the majority of hatched chicks fledge in most years (Hipfner et al. 2008), and so these mechanisms of sex ratio adjustment may be important. Sex allocation decisions might best be thought of as a continually modified allocation strategy, and the original hypotheses about important factors still apply.

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