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The triggers of fledging in Rhinoceros Auklets *Cerorhinca monocerata* chicks when they experienced mass recession, examined by a supplementary feeding experiment

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ORNITHOLOGICAL SCIENCE

Abstract Older or heavier Rhinoceros Auklet *Cerorhinca monocerata* chicks are less likely to remain in their nest during pre-fledging mass recession. Older or heavier chicks have longer wings but the individual variation in wing length at fledging is small. To identify proximate triggers of fledging from a mix of candidates when chicks experienced mass recession, we selected 30 nest boxes each containing a chick and provided half of them with 30–60 g of supplementary foods in an attempt to expand their variation in growth rate. When chicks reached the minimum wing length required for fledging (130 mm), we stopped all provisioning (supplementary and parental) by closing a hatch on the nest box entrance thereby simulating mass recession and inducing fledging. With these treatments, we examined whether timing of fledging (=duration of mass recession) was only triggered by wing length to a threshold size or whether timing of fledging was delayed by younger age at peak mass or lighter peak body mass. Our results indicate that younger chicks remained in their nests longer than older chicks at the beginning of pre-fledging mass recession, regardless of the small variation in wing length among individuals. Annual variation in the duration of mass recession was also detected but body mass was not the trigger for fledging. Measurement of baseline corticosterone level indicated a negative trend between the corticosterone level and the number of days between the measurement date and the fledging date.

Key words Age-dependent factor, Alcids, Pre-fledging mass recession, Wing length

Alcids show high within-population variation in the occurrence and degree of pre-fledging mass recession, which is associated with variation in fledging age and mass (Shultz & Sydeman 1997). Morbey et al. (1999) demonstrated two hypotheses to explain the variation in pre-fledging mass recession of Cassin's Auklets *Ptychoramphus aleuticus*. First, parents reduced provisioning to older or heavier chicks because the parental gain in fitness might be reduced by doing so as the chicks mature. Second, older or heavier chicks were more likely to depart from their nests during mass recession, because their survival prospects at sea were greater than those of younger or lighter chicks.

Parental regulation of provisioning according to the age and mass of the chicks is the key component of Morbey's hypotheses (Morbey et al. 1999). However, variation in parental provisioning according to chick age or mass was observed among experiments carried out on Atlantic Puffins *Fratercula arctica* and Rhinoceros Auklets *Cerorhinca monocerata* (Hudson 1979; Johnsen et al. 1994; Bertram et al. 1996; Cook & Hamer 1997; Erikstad et al. 1997; Takahashi et al.

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1999). Deguchi and Watanuki (2005) found that in Rhinoceros Auklets parental provisioning occurred regardless of chick age and mass, but older or heavier chicks were more likely to remain in their nests for a shorter time during mass recession than younger or lighter chicks.

Gliding and diving are essential abilities for alcid fledglings because they enable them to reach the sea safely from their nesting cliffs, escape from predators and collect food after fledging (Hedgren 1981; Clark & Ydenberg 1990; Øyan & Anker-Nilssen 1996; Hipfner & Gaston 1999). Individual variation in wing length is small at fledging in Atlantic Puffins and Rhinoceros Auklets (Barrett et al. 1987; Harfenist 1995; Deguchi et al. 2004; Takenaka et al. 2005; Sears & Hatch 2008). Fledglings Tufted Puffins *Fratercula cirrhata* with longer wings are more likely to survive and return to their natal colony (Morrison et al. 2009). Older or heavier Rhinoceros Auklet chicks have been shown to have longer wings (Takahashi et al. 1999; Deguchi et al. 2004), and this might explain why they remain in their nests for shorter times during mass recession.

Furthermore, elevated plasma baseline levels of the stress hormone corticosterone (associated with an increase in locomotion) have been shown to be positively correlated with age and negatively correlated with time before fledging (Astheimer et al. 1992; Heath 1997; Kern et al. 2001; Corbel & Groscolas 2008; Sprague & Breuner 2010).

In order to identify possible triggers for fledging during pre-fledging mass recession in the Rhinoceros Auklet, we experimentally controlled the growth rates of body mass and wing length of chicks by providing supplementary food and by inducing mass recession by stopping all provisioning when the chicks reached the minimum length required for fledging. In this way, we identified factors affecting the duration of pre-fledging mass recession. We also examined the relationship between stress hormone levels and the time before fledging.

MATERIALS AND METHODS

Rhinoceros Auklets are burrow-nesting seabirds that lay single-egg clutches. Chicks do not leave their nests prior to fledging. During chick rearing, adults deliver meals of 10–50 g, once a day after sunset on Teuri Island (44°25′N, 141°19′E) off northwest Hokkaido, Japan (Takahashi et al. 2001). The diet is composed mainly of Japanese Anchovy *Engraulis japonicus*, Japanese Sandlance *Ammodytes personatus*, and juvenile Arabesque Greenling *Pleurogrammus azonus*. Naturally reared chicks on Teuri Island typically fledged at an age of 40–70 days and at a body mass of 200–500 (Deguchi et al. 2004).

1) Food control experiment

We selected 30 nest boxes (Kuroki 1998), each containing a chick (16 in May 2002; 14 in May 2003 on Teuri Island. When chicks were first found, we used a ruler to measure their wing length to the nearest 1 mm and estimated their age using an equation reported in Takahashi et al. (2001). We weighed chicks daily to the nearest 1 g on a Pesola spring balance, and measured the natural wing length (chord) from the wrist to the wing tip every three days. Measurements were made between 1600 and 1800 JST prior to their parents returning from sea with food.

At the time of fledging, the wing length of more than 80% of wild Rhinoceros Auklet chicks on Teuri Island has been reported to be within the range of 130–150 mm (Deguchi et al. 2004). Therefore, we assumed that 130 mm was the minimum wing length required for fledging in this species. To expand the individual variation in age and body mass in chicks having an approximately equal-wing length at the beginning of pre-fledging mass recession, we manipulated the growth rate of body mass and wing length by providing supplementary food. In 2002, eight of 16 chicks (supplementary group) were provided daily with 40 g of additional food (Japanese Sandlance *Ammodytes personatus*), which is two thirds of daily meal mass for naturally reared chicks (Takahashi et al. 2001), in addition to parental provisioning from 20 days of age. Supplementary food was placed on the floor of each nest box after each chick had been measured; the chicks subsequently consumed the food. The control group (also 8 chicks) received food only from their parents and was not given additional food. In 2003, four out of 14 chicks were provided with 30 g additional food and a further five chicks were given 60 g of supplementary food daily from 20 days of age. The control group (the remaining five chicks) received food only from their parents. No difference in estimated hatching dates was observed between chicks that were provided with 40 g and no supplementary food in 2002 (t-test, $t=0.54$, $P=0.60$) and among chicks that were provided with 30 g, 60 g and no supplementary food in 2003 (ANOVA, $F_{2,11}=0.38$, $P=0.69$).

We set a plastic hatch (14 cm in diameter) at the nest box entrance (Kuroki 1998) on the day on which the chick's wing length reached or exceeded 130 mm. The hatch allowed the chick to depart from the nest box, but prevented the parents from entering the nest to provide food. We stopped providing supplementary food on the same day, but continued to weigh and measure the chicks every day until they fledged. Chicks were assumed to have fledged when they had disappeared from their nests. We expected that the group given supplementary food would be younger and heavier than the control group, but that they would have approximately equal wing lengths at the beginning of the pre-fledging mass recession.

2) Stress hormone

In order to gain additional information about baseline levels of the stress hormone corticosterone, we took whole blood samples (30–50 μl) in 2003 from chicks that were 0–14 days before they attained the age at peak mass. Samples were collected within 3 minutes of capture from the wing vein of every chick (30 g supplementary group: 36±3 days old, n=4; 60 g supplementary group: 33±1 days old, n=5; control group: 34±6 days old, n=5) by using a 27-gauge needle and a heparinized capillary tube. Capillary tubes were sealed with molding clay and stored on ice until returning to the field station. Blood was centrifuged and plasma was harvested and stored at −20 °C in a refrigerator until further assayed. Plasma corticosterone levels were estimated by a direct radioimmunoassay method (see Wada et al. 1999 for details). Sampling was conducted only once for each chick because repeated sampling results in reduced baseline corticosterone level (Love et al. 2003).

3) Statistical analysis

We used a generalized linear model with a Poisson error distribution and a log link function to identify the factors affecting the duration of pre-fledging mass recession as fledging age minus age at peak body mass (Morbey et al. 1999). We pooled sampling years because of the small sample size and used age, body mass, wing length of chicks when they reached peak body mass, group (40 g, 30 g, and 60 g supplementary and control group) and year as explanatory variables. Among the explanatory variables, there was a negative trend between age and body mass (Pearson correlation test, $r=-0.40$, $P=0.06$), but no correlations between age and wing length ($r=0.23$, $P=0.27$) or between body mass and wing length ($r=0.17$, $P=0.42$). If chicks remain in their nests only to reach the wing length required for fledging while losing mass under natural conditions, no significant effects of age or mass on this duration of mass recession was expected. In contrast, if younger or lighter chicks whose wings reached that length remained longer in their nests under natural conditions, a significant effect of age or mass on this duration should occur. In 2002, two chicks (one each from the supplementary and control groups) disappeared from their nests before their wings reached lengths of 130 mm. The same was true for 2 chicks each from the 30 g and 60 g supplementary groups in 2003. Information on how they were lost is not available; hence, these data were excluded from the analysis. Five chicks in the supplementary group and two chicks in the control group in 2002, and three chicks in the control group in 2003 attained age at peak body mass 1–7 days before their wing length reached 130 mm. For the remaining 14 chicks, age at peak mass coincided with the age when their wings reached this length.

We based the final model selections on Akaike's information criterion (AIC). We analyzed all possible combinations of explanatory variables and selected the model with the smallest AIC as the best fitting model and considered models with ΔAIC <2.0 to be competing models with little difference from the best one (Burnham & Anderson 1998).

We used ANOVA for comparing plasma corticosterone levels among 30 g, 60 g supplementary and control group, and Pearson correlation test for examining the relationship among the corticosterone level, age, body mass, wing length on the measurement date and the number of days from the measurement date to the fledging date. We used SPSS version 20.0 for all statistical analyses. Data are presented as means±SD.

RESULTS

As expected, supplementary groups were younger and heavier than control groups but small differences in wing length among chicks at the beginning of pre-fledging mass recession occurred, except in the 30g supplementary group in 2003 (Fig. 1; Table 1).

The competing models to explain factors affecting the duration of pre-fledging mass recession included both age and year (Table 2). These results indicated that older chicks fledged sooner when they experienced mass recession (Fig. 2) and that the duration of pre-fledging mass recession varied between years (2002: 4±2 days; 2003: 6±3 days).

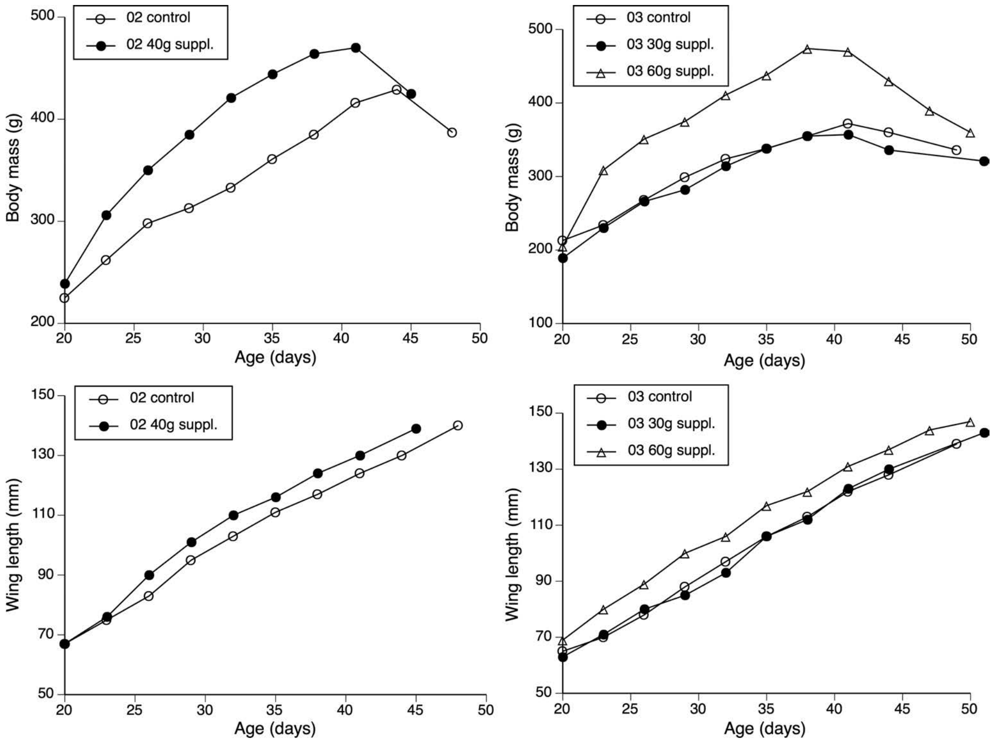

Fig. 1. Mean body mass (upper) and wing length (lower) of 30 g, 40 g, 60 g supplementary feeding and control group Rhinoceros Auklet chicks on Teuri Island (23 May–9 July 2002 and 9 June–17 July 2003). Every terminal symbol indicates mean age and body mass or wing length at fledging.

Table 1. Mean and (range) of age, body mass and wing length of 40 g, 30 g, 60 g supplementary feeding and control group Rhinoceros Auklet chicks when they reached the age at peak body mass and fledged on Teuri Island (13 June–9 July 2002 and 29 June–17 July 2003).

	2002		2003		
	Control (n=7)	40 g suppl. (n=7)	Control (n=5)	30 g suppl. (n=2)	60 g suppl. (n=3)
Age at peak body mass (days)	44 (42–48)	40 (38–44)	43 (40–52)	47 (40–53)	41 (40–43)
Peak body mass (g)	449 (393–514)	485 (426–570)	397 (284–461)	377 (304–449)	480 (464–505)
Wing length at peak body mass (cm)	131 (123–136)	127 (120–131)	130 (123–133)	132 (130–133)	133 (131–134)
Age at fledging (days)	48 (45–50)	45 (42–48)	49 (45–56)	51 (45–56)	50 (48–53)
Body mass at fledging (g)	387 (325–484)	425 (362–470)	336 (260–400)	321 (267–374)	360 (341–390)
Wing length at fledging (mm)	140 (137–143)	139 (131–144)	139 (136–144)	143 (139–147)	147 (144–151)

No significant differences were found in the plasma corticosterone levels among the 30 g (88.9±19.4 ng/ml), 60g supplementary (60.7±19.7 ng/ml) and control group (71.2±25.8 ng/ml) ($F_{2,11}=1.82$, $P=0.21$). There was a negative relationship between the corticosterone level and the number of days from the measurement date to the fledging date ($r=-0.50$, $P=0.07$, Fig. 3); however, no correlation was observed between the corticosterone level and age ($r=0.11$, $P=0.72$), body mass ($r=0.05$, $P=0.86$), or wing length ($r=0.29$, $P=0.32$).

DISCUSSION

At the beginning of pre-fledging mass recession, younger chicks remained in their nest longer than older chicks, regardless of the small differences in wing length among them. However, body mass was

Table 2. Generalized linear model selection results for factors affecting the number of days from the date of age at peak mass to fledging date in Rhinoceros Auklet chicks (n=24) on Teuri Island (13 June–9 July 2002 and 29 June–17 July 2003). Explanatory variables in the model include age, body mass, wing length, group (40 g, 30 g, 60 g supplementary feeding, and control group) and year. Only models with differences in Akaike's Information Criterion (ΔAIC<2) are listed. We also present Akaike weights (w_i). Significance of each model was obtained from a likelihood ratio test comparing with the null model.

Coefficient estimates					Log likelihood	ΔAIC	w_i	χ^2	P
Age	Body mass	Wing length	Group	Year*					
−0.072				−0.367	−48.314	0	0.214	10.257	<0.01
−0.068	0.001			−0.394	−48.247	1.865	0.084	10.392	0.02
−0.071		−0.003		−0.374	−48.308	1.988	0.079	10.269	0.02

*The coefficient of this variable indicates value for 2002 data.

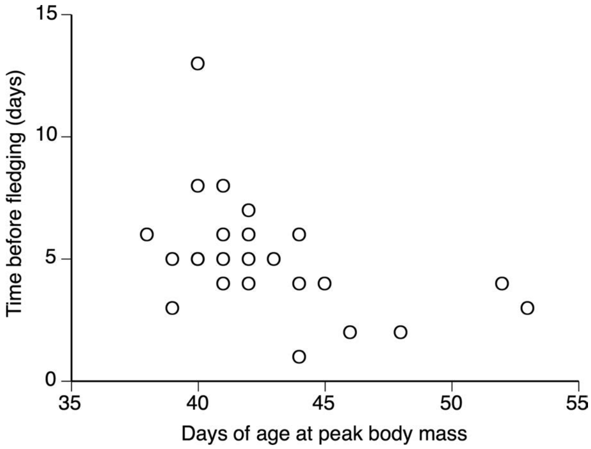

Fig. 2. Relationship between the time before fledging and age at peak body mass in Rhinoceros Auklet chicks on Teuri Island (13 June–9 July 2002 and 29 June–17 July 2003).

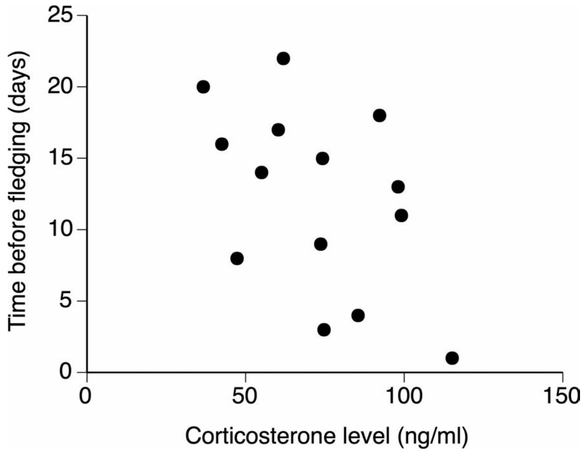

Fig. 3. Relationship between plasma corticosterone level and the number of days from measurement date to fledging date in Rhinoceros Auklet chicks (28–43 days old) on Teuri Island (24 June-17 July 2003).

not the trigger for fledging. These results suggest that the timing of fledging of Rhinoceros Auklet chicks was determined not only by their wing length (Deguchi & Watanuki 2005), but also by the age at which they experienced mass recession. It is unclear why younger chicks, which are not more likely to be fed by parents than older chicks (Deguchi & Watanuki 2005), remained longer in their nests. A possible cause is the secretion of the stress hormone corticosterone, which promotes fledging behaviour. Levels of this hormone have been found to be positively correlated with age in American Kestrel *Falco sparverius* chicks and in Laysan Albatross *Phoebastria immutabilis* chicks (Heath 1997; Wada 2008; Sprague & Breuner 2010). However, our results did not support involvement of stress hormones with age, although our lack of results could result from our small sample sizes as there is known to be high individual variation in baseline corticosterone level (Romero & Reed 2008).

In addition to the wing length at fledging, the functional maturity of other tissues, the body plumage, and the central nervous system are probably important for fledging (Hipfner & Gaston 1999). The time required for these tissues to mature might influence the timing of fledging. Younger chicks with the wing length required for fledging might need to remain in their nests longer than older chicks because of this need for tissue maturity. Øyan and Anker-Nilssen (1996) have suggested that growth of the head is given the highest priority in food stressed Atlantic Puffin chicks, which probably reflects the importance of a well-developed brain and nervous system. Since Atlantic Puffin chicks do not receive parental care after fledging (Harris & Birkhead 1985), they are forced to acquire skills involved in pursuing and capturing prey very quickly. Takenaka et al. (2005) found similar results to those of Øyan & Anker-Nilssen (1996) including less variation in head growth using food-controlling experiments in Rhinoceros Auklet chicks. Whereas naturally reared chicks typically fledge at 52±7 days (Deguchi et al. 2004), fledging age in our study involving providing additional food was younger, averaging 48±3 days. This result may partially support the finding that the time required for tissue maturity is important for the timing of fledging in our study chicks.

The duration of pre-fledging mass recession was shorter in 2002 than 2003, but it is unclear why this was so. The difference between years in the mass growth rate in the control groups indicates that the parental provisioning rate was higher in 2002 than 2003 (Fig. 1). Higher parental investment might suggest that chicks decide to fledge sooner than those that receive lower parental investments when they experienced mass recession. Future work to corroborate this hypothesis is warranted. Our results suggest that the triggers of fledging when Rhinoceros Auklets chicks experience mass recession include a combination of wing length, age-dependent functional maturity of other tissues and parental provisioning.

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