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Parental provisioning, nestling departure decisions and prefledging mass recession in Cassin's auklets

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We investigated how parental provisioning and nestling departure behaviour interact to produce prefledging mass recession in Cassin's auklets, *Ptychoramphus aleuticus*. Under our hypothesis, auklet parents are reluctant provisioners and should be increasingly likely to terminate or reduce provisioning of their single nestling as it matures. For the nestling, remaining in the nest presents a risk of losing mass (if the parent does not provision) but also a possibility of additional provisioning. As the nestling matures and becomes increasingly capable of independence, the benefits of remaining in the nest decrease and nestlings should be increasingly likely to fledge. Nestlings also should be more likely to fledge when the expectation of additional provisioning is low. Data on parental provisioning (based on growth increments) and nestling departure were consistent with our hypothesis. Older and heavier nestlings had smaller growth increments than younger and lighter nestlings, suggesting that parents were reluctant to provision old and heavy nestlings. Older and heavier nestlings also were increasingly likely to fledge. We hypothesized that nestlings might use the intensity of mass loss to gauge parental reluctance to provision, and accordingly, nestlings were increasingly likely to fledge after experiencing a greater amount of mass loss.

Nestlings in a variety of avian groups, including swallows, swifts and seabirds, lose mass prior to leaving their nests for the outside world (Ricklefs 1968; Sealy 1973). Species in the family Alcidae show tremendous intraspecific variation in the occurrence and degree of mass loss (e.g. Morbey 1995 for Cassin's auklets, *Ptychoramphus aleuticus*), and in other aspects of their nest departure behaviour (Ydenberg et al. 1995). None of the various hypotheses put forward to explain mass recession addresses this variation. In this paper we focus on the interaction of parent and nestling alcids in an attempt to understand the adaptive significance (i.e. the selective factors responsible for its evolution) of prefledging mass recession, and how the large intraspecific variation observed may arise.

Four hypotheses have been proposed to explain prefledging mass recession. According to the 'wingloading hypothesis,' losing surplus fat and thus lowering the wing area to body mass ratio is necessary for flight or diving following nest departure (cf. Ricklefs 1968; Pennycuick 1972; Martins 1997). Another hypothesis is that nestlings require a longer period of structural development than that provided by parents to ensure their postdeparture survival. Yet another explanation for mass recession, the 'flexible timing hypothesis', is that by delaying fledging after parents have ceased provisioning, the nestling may be able to select an advantageous moment to fledge, a dark night for example, or, in colonial species, when many other nestlings are also departing (e.g. Daan & Tinbergen 1979).

Ydenberg (1989) presents an adaptive explanation for prefledging mass recession that differs from the previous hypotheses because it incorporates parental provisioning behaviour and nestling departure behaviour. Clark & Ydenberg (1990) modelled this dynamic interplay between parental provisioning and nestling fledging behaviour. One important assumption of their model was the existence of a fledging mass constraint. Parents were predicted to provision nestlings beyond the nestling's optimal fledging mass. Thus 'overfed' nestlings would take advantage of the relative safety of the nest burrow, residing there until they fell to the optimal fledging mass.

We present a different hypothesis for prefledging mass recession based only on general assumptions. Our most basic assumption is that in deciding whether to make a provisioning visit to the nest, parents evaluate the benefits and costs in fitness terms. The benefit of a

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provisioning visit is an increase in the nestling's postdeparture survival prospects. Beyond a certain minimum age and mass, however, we assume that there are diminishing returns so that the marginal benefit of a provisioning visit to a small nestling is greater than to a large nestling of the same age, and the marginal benefit of a provisioning visit to an old nestling is smaller than to a young nestling of the same mass. The costs of a provisioning visit must also be considered. The most important of these, and the only one we consider here, is that parents may risk depredation when they visit the nest (Harfenist & Ydenberg 1995). The risk may vary with conditions such as weather, moonlight and exact nest location, but we assume that it is not dependent on nestling size or age. This risk makes parents calculating provisioners, and they provision only when the expected net benefit, from their point of view, is positive.

We assume that auklet nestlings assess the net benefit of continued residence, and leave when departure gives greater expected fitness. The benefit of staying is that a later delivery may be enjoyed in the safety of the nest burrow, but there is also a cost: if parents fail to visit or deliver reduced amounts of food, the nestling foregoes the opportunity to be growing at sea and must live from its reserves. The best action for a nestling to take is complicated by the uncertainty associated with parental provisioning. There can be considerable stochasticity in the frequency and quantity of food deliveries (e.g. for rhinoceros auklets, *Cerorhinca monocerata*: Bertram et al. 1988; Harfenist 1991). Under the assumption that parents are calculating provisioners, nestlings cannot be certain, following the failure of an anticipated visit or a greatly reduced load size, that parents will not provision again.

If the expectation of more provisioning is high, the nestling should remain, but if the expectation is low, perhaps indicated by a long absence of parents or a steep decline in the amount of food recently delivered, nestlings should depart. The departure decision also may depend on the expectation of growth at sea after nest departure. Small or young nestlings or those in poor condition benefit more from provisioning visits, probably have lower postdeparture survival prospects, and so are more likely to tolerate mass loss. In contrast, food deliveries benefit older or heavier nestlings less, and so they are less likely to tolerate mass loss.

We suggest that the parents' and nestling's assessments of the costs and benefits interact to produce prefledging mass recession. Under our hypothesis, we expect parents to provision older and heavier nestlings less frequently. For a given nestling age and mass, parents should visit the colony less frequently in habitat that poses greater predation risk to themselves. Nestlings should tolerate mass loss less frequently when they are older, heavier, or when losing mass rapidly. We use data on growth and fledging of Cassin's auklets to discriminate among our hypothesis and the four alternative hypotheses.

METHODS

We studied the growth and fledging of nestling Cassin's auklets on Triangle Island, British Columbia in 1994 (Y.E.M). Cassin's auklets are long-lived seabirds and typically raise a single nestling per year. Nestlings have semiprecocial development, and after nest departure, young are apparently independent (Manuwal & Thoresen 1993). Prior to nest departure, nestlings typically lose mass (Sealy 1973; Vermeer & Cullen 1982; Morbey 1995). Additional information about the natural history of Cassin's auklets is available in Manuwal & Thoresen's (1993) species account. We located nestlings in either level (N=45) or steep habitats (N=107), which represent dangerous and safe habitats, respectively, from the parent's perspective (Morbey & Ydenberg 1997). We measured nestling mass and wing (chord) length at regular intervals (methodology described in Morbey & Ydenberg 1997).

Analyses presented here include all nestlings that fledged (N=152, five nestlings with 'shut-eye' disease were excluded, see Morbey 1996). In these analyses, we used the last recorded age and mass for fledging age and fledging mass (± 0.5 g). Because nestlings were measured every second day near fledging, a nestling that was last measured on day i could have fledged on night i or night i+1. We labelled nestlings as having experienced prefledging mass recession if any previously attained mass exceeded fledging mass. We defined the amount of mass recession as peak (maximum) mass minus fledging mass, and the duration of mass recession as fledging age minus age at peak mass. If peak mass occurred at more than one age, we labelled the oldest age as the age at peak mass. An 'observation' refers to the nestling's characteristics measured during a single visit to its nest burrow.

Parental Provisioning

In the absence of direct data on parental provisioning, we used growth of nestlings to infer parental provisioning behaviour. Growth (g/day) between the current (j) and the next burrow check (j+1) was estimated as $(\text{mass}_{j+1} - \text{mass}_j)/(\text{age}_{j+1} - \text{age}_j)$ and will be referred to as succeeding growth. We assumed a positive correlation existed between succeeding growth and amount provisioned (cf. Ricklefs et al. 1985; Bertram et al. 1996).

We determined how nestling age and mass affected succeeding growth and whether these effects differed among the habitat types (level versus steep) using ANCOVA. We began with a fully saturated statistical model which included nestling age and mass as continuous variables, habitat type as a class variable, and the two interaction variables (habitat × nestling age and habitat × nestling mass). Nonsignificant interaction variables were sequentially dropped from the saturated model. After one variable was dropped, the reduced model was reanalysed before assessing the significance of the remaining variables. To avoid pseudoreplication arising from repeated observations per nestling, we randomly selected a single observation per nestling and computed the F statistic. We repeated the randomized selection and analysis 100 times and generated the P value from the mean F statistic (Robertson et al. 1994). Positive succeeding growth dominated the nestlings' growth trajectories up until approximately 30 days of age, suggesting that parents provisioned regularly up until this point. We sought to explain the variation in succeeding growth during the prefledging period and so only included observations with ages of 30 days or more in our analyses. We predicted that succeeding growth would decrease with nestling age and mass and that these effects would be greater in level habitat than in steep habitat, because level sites presented greater risks to parents.

We used logistic regression to corroborate the results of the analysis of variance. The difference between these two approaches is simply that the analysis of variance considers the magnitude of succeeding growth, whereas the logistic regression categorizes succeeding growth as positive or negative. If succeeding growth was positive or zero, we assumed parents had provisioned the nestling; if negative, we assumed parents had not provisioned the nestling. We used the randomized selection procedure outlined above, repeated the analysis 100 times, and generated *P* values for the overall model and partial effects from the mean χ^2 statistics. The parameter estimates were obtained for the logit transformation of the logistic model, where the dependent variable is $\mathrm{logit}(p)=\ln(p/(1-p))$, and p is the critical probability value in classifying an event (provision) or nonevent (do not provision). We predicted that the probability of provisioning would decrease with nestling age and nestling mass.

Nestling Departure

To investigate why nestlings tolerated mass loss, we used logistic regression to examine how nestling state (nestling age and mass) and recent growth influenced the probability of fledging (fledging is the event and staying is the nonevent). For each burrow check i, we calculated growth (g/day) from the first ($j=i-1$), second ($j=i-2$), and third ($j=i-3$) most recent checks as $(\mathrm{mass}_i-\mathrm{mass}_j)/(\mathrm{age}_i-\mathrm{age}_j)$. We will refer to this measure as preceding growth to distinguish it from succeeding growth. To isolate observations with mass loss, we included only those observations where nestlings had lost mass from the previous check. A nestling was associated with fledging at a particular check if at the next check, it had departed. Otherwise, it was recorded as staying.

We began with a saturated logistic regression model which included nestling age, mass and preceding growth since the first, second and third most recent burrow checks. Nonsignificant variables were sequentially dropped from the saturated model. After one variable was dropped, the reduced model was reanalysed before assessing the significance of the remaining variables. We used the randomized selection procedure outlined in the parental provisioning section to avoid pseudoreplication. The *P* values were generated from the mean χ^2 statistics. We present the parameter estimates for the logit transformation of the logistic model. If nestlings anticipate parental provisioning based on their current state, we expected the probability of fledging to increase with nestling age and mass. If nestlings use preceding growth to anticipate parental provisioning, we expected the probability of fledging to decrease with preceding growth.

Comparative Patterns of Mass Recession

We tested predictions about the intraspecific patterns of mass recession using the current data set and additional growth data for Cassin's auklets from Triangle Island in 1995 ($N=73$, H.A.K.) and Frederick Island, British Columbia in 1996 ($N=113$, A.H.). We chose the rate of mass recession (amount divided by duration of mass recession, g/day) to represent parental provisioning. (The rate of mass recession in relation to the age of peak mass is analogous to succeeding growth; the rate of mass recession in relation to fledging age is analogous to preceding growth.) If parents provision heavy and old nestlings less frequently, we would expect the rate of mass recession to increase with age at peak mass (prediction 1) and with peak mass regardless of age (prediction 2). If nestling state and recent growth affect the fledging decision in the predicted way, we would expect nestlings to tolerate a shorter duration of mass recession with increasing age at peak mass (prediction 3), increasing peak mass (prediction 4), and increasing rate of mass recession (prediction 5). These predictions were analysed using linear regression for each study. We only included nestlings with mass recession in the analyses. Problems with high residuals were expected because peak mass and age at peak mass were not normally distributed. Individual observations that had large studentized residuals (>2 or <-2) were dropped from the model and the regression models were refit once (SAS 1990). We did not include quadratic or other higher-order terms in these analyses to simplify the interpretation of the results. Furthermore, we were testing for the directionality of the effect, and visual examination of the residual plots indicated that the partial effects were monotonic.

The Wingloading Hypothesis

Under the wingloading hypothesis: (1) nestlings without mass recession should have a lower peak mass than nestlings with mass recession; (2) wingloading should be higher in level habitat than in steep habitat; and (3) with increasing nestling mass, the amount of mass loss should increase, but wingloading at fledging should be constant. To test this idea, we estimated wingloading at fledging as fledging mass/fledging wing^2, where fledging wing (± 0.5 mm) is the last recorded wing length. (The optimal wingloading at fledging is unknown for Cassin's auklets, and there is uncertainty over which aspect of flight or diving should be optimized. For this reason, we did not derive a more complex estimate of wingloading.) The predictions were tested using linear regression analysis or ANOVA where appropriate.

We used SAS statistical software for all analyses (SAS 1990). The significance levels used for the stepwise regression models were $\alpha=0.5$ for entry and $\alpha=0.05$ for removal (Myers 1990). For the logistic regressions, we present the χ^2 associated with the -2 log-likelihood statistic. We used $\alpha=0.05$ as the significance level for the rest of the analyses. We present *F* statistics based on partial (type III) sum of squares for ANOVAs and ANCOVAs, and *t* statistics (two-tailed) and coefficient of determination (R^2) for

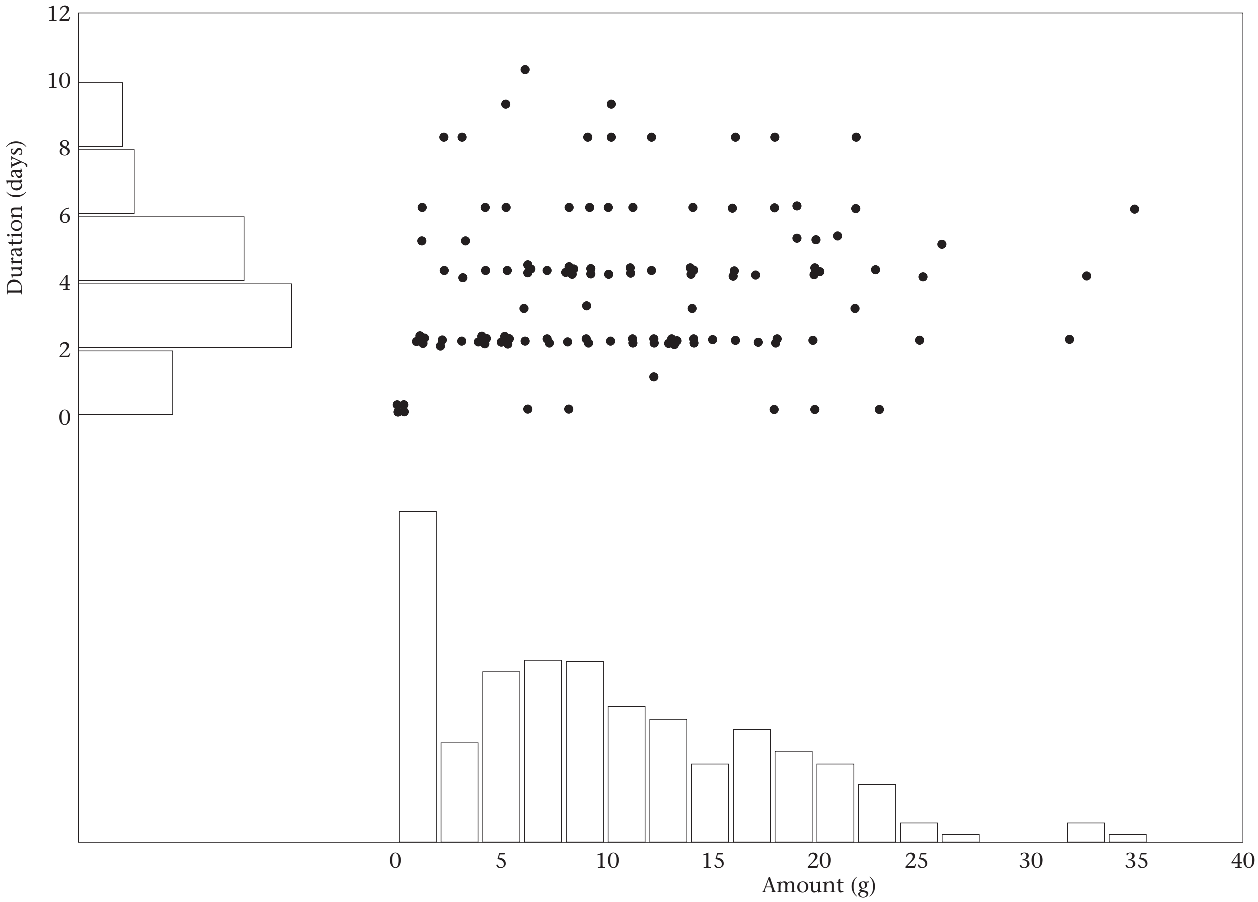

Figure 1. Frequency distributions and bivariate scatterplot of the duration and amount of mass recession (N=151; data missing for one nestling). In the scatterplot, points have been offset to better display overlapping data.

the linear regression models. When the randomized selection procedure was used to generate P values, we also present the range of the F or χ^2 statistics.

RESULTS

General Observations

We observed large intraspecific variation in the occurrence and degree of mass recession in Cassin's auklets (Fig. 1). The amount and duration of mass recession were variable and not normally distributed; the median amount of mass recession was 10 g (6% of mean fledging mass) and the median duration of mass recession was 4 days (9% of mean fledging age). Mass recession occurred more frequently in level habitats (96%, N=45) than in steep habitats (80%, N=107; χ^2_1=5.685, P<0.05).

Parental Provisioning

In the prefledging period (i.e. between 30 days of age and nest departure), age and mass influenced parental provisioning as predicted. Heavier nestlings had slower succeeding growth than lighter nestlings of the same age, and older nestlings had slower succeeding growth than younger nestlings of the same mass (Table 1, Fig. 2). These effects did not differ among habitats (habitat × nestling mass: $F_{1,141}$=0.901 (range 0.000–6.319), NS; habitat × nestling age: $F_{1,142}$=2.080 (range 0.000–13.891), NS) nor did succeeding growth differ among habitats (Table 1). The logistic model gave similar results. Age and mass influenced the probability of parental provisioning as predicted (χ^2_2=27.696 (range 7.333–50.894), P<0.001). Heavier and older nestlings were increasingly likely to lose mass (mass effect: χ^2_1=9.293 (range 0.302–26.472); age effect: χ^2_1=9.096 (range 0.307–25.575), P<0.01; Fig. 2).

Table 1. Analysis of variance of succeeding growth as a function of nestling age, mass and habitat (level versus steep)

Source	*df*	SS	*F* (range)
Age	1	122.955	11.466 (1.711–43.481)*
Mass	1	167.969	15.715 (2.563–36.839)*
Habitat	1	10.222	0.953 (0.000–6.109)
Error	143	1558.18	

*P<0.001.

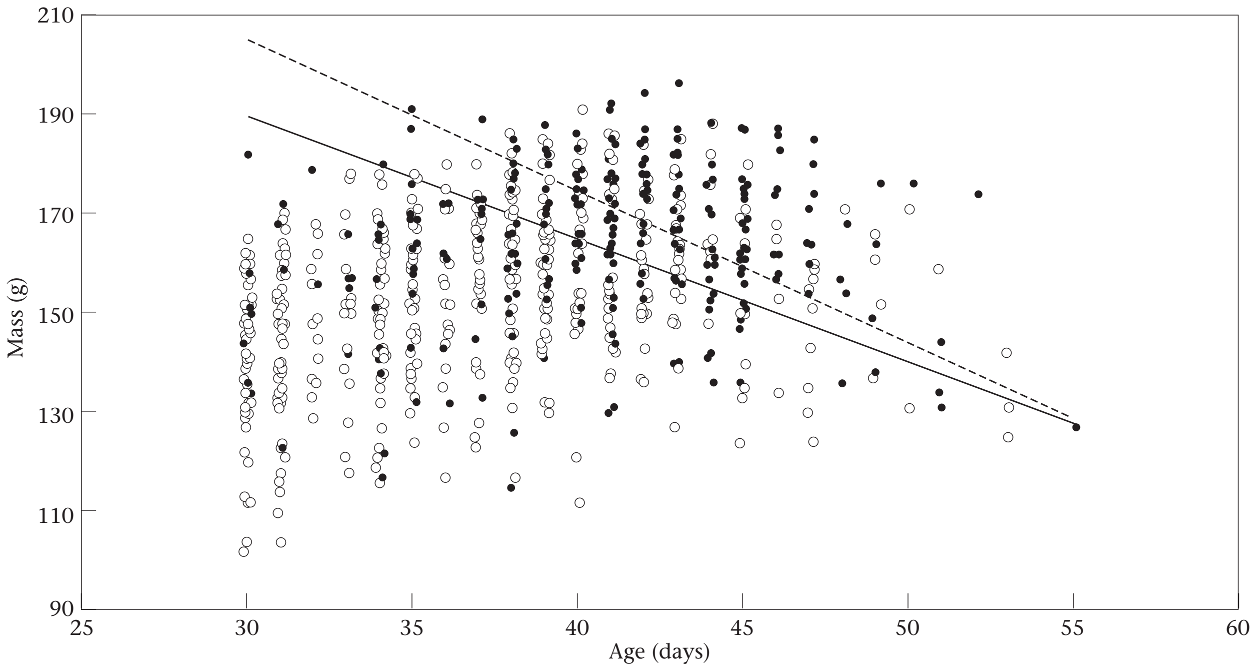

Figure 2. Positive (○) and negative (●) succeeding growth for all nestlings as a function of their mass and age. Each observation (2–10) of each nestling is shown here, but analyses used a single randomly chosen observation per nestling. The solid line shows mass and age combinations above which succeeding growth is expected to be less than zero (i.e. more shaded circles are located above the line than below). The parameter estimates for this line were obtained from the general linear model (succeeding growth=19.256−0.180×nestling age−0.073×nestling mass). The dashed line shows mass and age combinations above which the probability of provisioning is less than 0.5. The equation of this line was obtained using the parameter estimates from the logistic regression (logit(p)=13.239−0.136×nestling age−0.045×nestling mass) and specifying 0.5 as the critical probability value. Note the similarity between the two sloped lines. Data points have been offset to better display overlapping data.

Table 2. Logistic regression analysis of the effect of nestling age, nestling mass and preceding growth (from the second most recent burrow check) on the probability of fledging

Source	Estimate	Standard error of estimate	Wald χ^2_1 (range)
Intercept	−23.363	5.784	16.261 (10.659–20.485)*
Age	0.306	0.085	12.979 (5.531–18.067)*
Mass	0.057	0.021	7.396 (1.697–14.043)*
Preceding growth	−0.714	0.160	19.741 (12.458–26.457)*

*$P<0.001$.

Nestling Departure

Age, mass and preceding growth from the second most recent burrow check influenced the probability of fledging (χ^2_3=72.469 (range 50.487–100.957), $P<0.001$) (Table 2, Fig. 3). Nestlings were increasingly likely to fledge when they were older and heavier. The more mass a nestling lost from the second most recent burrow check, the greater the probability it fledged. Preceding growth from the first and third most recent burrow checks did not influence the probability of fledging.

Comparative Patterns of Mass Recession

Nestling growth data from Triangle Island in 1994 and 1995, and Frederick Island in 1996 generally supported the predictions about the patterns of mass recession (Table 3). The rate of mass recession increased with peak mass and age at peak mass in all three studies, supporting our hypothesis that parents are increasingly reluctant to provision old and heavy nestlings.

Nestlings that were older at their peak mass had a shorter duration of mass recession in all three studies, supporting our hypothesis that age influences departure decisions. The effect of age at peak mass on departure decisions appears to be much stronger than the effect of peak mass or rate of mass recession. In each of the three studies, age at peak mass accounted for most of the variation in the duration of mass recession. The proportion of the variance explained by peak mass and rate of mass recession were low in each study (with one exception), but the significant effects were in the

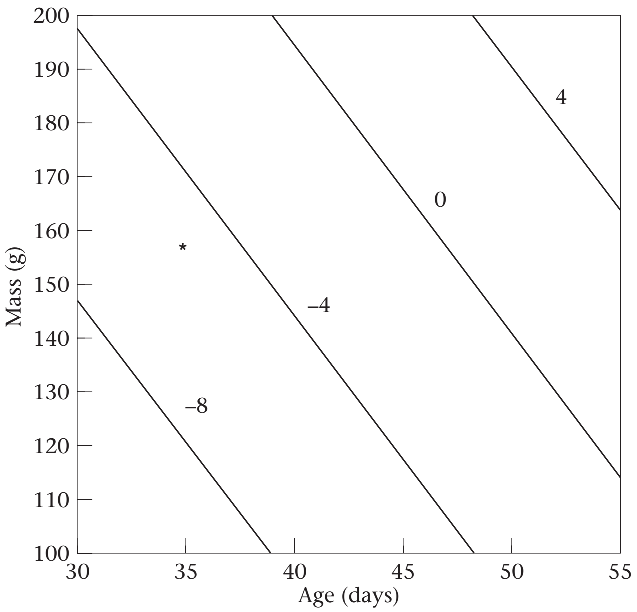

Figure 3. Representation of nestling departure decisions as a function of nestling age, nestling mass and preceding growth (diagonals). Preceding growth is from the second most recent burrow check. For values of preceding growth spanning the range observed (−8–4 g/day), diagonals show mass and age combinations above which the probability of fledging is greater than 0.5. Each diagonal was estimated from the data using the parameter estimates from the logistic regression (Table 2) and specifying 0.5 as the critical probability value. The probability of fledging increases with nestling age, nestling mass and preceding growth. For example, a hypothetical nestling weighing 157 g at 35 days of age (asterisk) would be more than 50% likely to fledge if it lost 8 g since the second most previous nest check. If it lost only 4 g, however, if would be less than 50% likely to fledge.

expected direction. Heavier nestlings of similar age fledged sooner than lighter nestlings on Triangle Island in 1994 and 1995 but not on Frederick Island in 1996. Nestlings with a faster rate of mass recession fledged sooner on Triangle Island in 1994 and Frederick Island in 1996 but not on Triangle Island in 1995.

The Wingloading Hypothesis

None of the three predictions of the wingloading hypothesis was upheld. First, nestlings without mass recession did not have a lower peak mass than nestlings with mass recession (ANOVA: $F_{1,149}$=0.38, NS). Second, wingloading at fledging did not differ between level and steep habitats ($F_{1,149}$=0.83, NS). Finally, although nestlings with heavier peak masses lost more mass than lighter nestlings (*t* test: t_{142}=8.843, P<0.001), they fledged with greater wingloading (*t* test: $t_{142}=-9.397$, P<0.001) (ANOVA: $F_{2,142}$=53.575, P<0.001, R^2=0.430, six influential observations removed). Furthermore, unlike other seabirds with prefledging mass recession (Table 2 in Ricklefs 1968), the peak masses attained by nestlings on Triangle Island in 1994 rarely surpassed average adult mass during the breeding season (ca. 190 g), suggesting that nestlings were not overburdened by excess fat.

DISCUSSION

Our data support the hypothesis that parental provisioning behaviour and nestling departure decisions interact to cause prefledging mass recession. It appears that, in the late phase of burrow residence, parents feed heavier nestlings less frequently than lighter nestlings of the same age, and feed older nestlings less frequently than younger nestlings of the same mass. Nestlings fledge more readily following mass loss when older, heavier, or after experiencing greater mass loss. These results are consistent with our hypothesis that nestlings consider the net benefit of staying in the nest versus departing.

We expected older and heavier nestlings to depart more readily following mass loss because of the diminishing returns associated with continued growth in the nest. Age appears to have had the strongest and most consistent effect on nestling departure decisions. Older nestlings,

Table 3. Linear regression analysis of rate of mass recession and the duration of mass recession on Triangle Island (1994 and 1995) and Frederick Island (1996)

	Triangle Island 1994	Triangle Island 1995	Frederick Island 1996
Prediction	*t* test, partial R^2	*t* test, partial R^2	*t*-test, partial R^2
Rate of mass recession increases with age at peak mass	t_{114}=2.381* R^2=0.047	t_{41}=2.408* R^2=0.124	t_{95}=5.655*** R^2=0.252
Rate of mass recession increases with peak mass	t_{114}=5.764*** R^2=0.226	t_{41}=2.547* R^2=0.137	t_{95}=5.039*** R^2=0.252
Duration of mass recession decreases with age at peak mass	t_{112}=−6.955*** R^2=0.302	t_{39}=−16.409*** R^2=0.873	t_{94}=−18.096*** R^2=0.777
Duration of mass recession decreases with peak mass	t_{112}=−2.672** R^2=0.060	t_{39}=−5.707*** R^2=0.455	t_{94}=−0.366 R^2=0.001
Duration of mass recession decreases with rate of mass recession	t_{112}=−3.487*** R^2=0.098	t_{39}=0.604 R^2=0.009	t_{94}=−4.467*** R^2=0.175

*P<0.05, **P<0.01, ***P<0.001.

controlling for mass and intensity of mass loss, fledged more readily than younger nestlings in the detailed analysis of nestling departure decisions. Nestlings that were older at their peak mass, controlling for peak mass and the rate of mass loss, also fledged sooner than younger nestlings in the comparative analyses. Nestlings also considered their own mass in their departure decisions but the effect was weaker than for age. Nestlings were more likely to fledge (after losing mass) if they were heavier at a given age and intensity of mass loss according to the detailed analysis, and heavier nestlings tolerated a shorter period of mass recession before fledging in two of the three studies examined in the comparative analyses. On Frederick Island in 1996, the strong dependence of mass recession duration on age at peak mass and rate of mass recession perhaps overshadowed any effect of peak mass.

We expected parental behaviour (i.e. provisioning) and nestling condition to influence the departure decisions of nestlings. But how do nestlings assess whether their parent will return or not? Nestlings seemed to use the intensity of mass loss to gauge parental reluctance to provision. Nestlings with a faster rate of mass recession fledged sooner in two of the three studies, and nestlings that lost more mass since the second most recent burrow check were more likely to fledge. Shorter-term information (i.e. growth since the previous burrow check) did not factor into the fledging decision perhaps because it predicts future provisioning less reliably. Again, as suggested for nestling departure decisions on Frederick Island in 1996, the highly significant effects of peak mass and age at peak mass may have overshadowed any effect of rate of mass recession on the duration of mass recession on Triangle Island in 1995.

Remaining in the burrow to await a possible provisioning visit makes sense only if the nonarrival of parents on the preceding night does not necessarily mean they have terminated provisioning (otherwise the nestling should depart). Many nestlings (82/152 or 54%) regained mass following mass loss at some point throughout their nest residence, suggesting that parents do provision irregularly. Bertram et al. (1988) and Harfenist (1991) also observed extensive variation in the size of loads delivered to nestling rhinoceros auklets. Irregular provisioning could result from stochastic foraging success, a reluctance to provision, or both. Many authors have emphasized the importance of stochasticity in foraging success as a important feature of seabird life histories (e.g. Clark & Ydenberg 1990; Ricklefs & Schew 1994).

Stochastic foraging success may account for some instances of mass loss, but adaptive provisioning behaviour is the more likely explanation for the prevalence of prefledging mass recession. Instances of mass loss would have been distributed randomly with respect to nestling age if provisioning was subject only to stochastic events. However, the probability that nestlings lost mass increased with nestling mass and age. Rate of mass recession also increased with peak mass and age at peak mass during the three studies examined. Seabird studies measuring provisioning rates also report a decrease in provisioning frequency with nestling age (Ashcroft 1979; Ricklefs et al. 1980; Henstridge & Tweedie 1984) or more generally, a modification of parental provisioning behaviour dependent on nestling need (Hudson 1979a; Harris 1983; Johnsen et al. 1994; Bolton 1995; Bertram et al. 1996; Erikstad et al. 1997; but see Ricklefs 1987; Hamer & Hill 1994). We find it unlikely that mass loss is due to voluntary rejection of food by nestlings. Harris (1978) and Hudson (1979b) observed prefledging mass recession in puffin, *Fratercula arctica*, nestlings experimentally provided supplementary food throughout their nest residence, and rejection of food by nestlings contributed at least to part of this decline. However, the amounts of food provided greatly exceeded normal provisioning levels. We are not aware of any direct evidence that seabird nestlings reject food when experiencing normal provisioning levels.

We expected parental provisioning late in the nestling period to depend on predation risk. We observed more cases of mass recession in the level (dangerous) habitat than in the steep habitat, which is consistent with parents terminating provisioning earlier when facing greater predation risk. However, we could not detect an effect of predation risk in the extensive analyses of parental provisioning. Using the same sample of nestlings, Morbey & Ydenberg (1997) showed that slow-growing nestlings fledged at younger ages in level habitat than in steep habitat but nestlings in both habitats fledged at similar masses, suggesting that parents terminated provisioning earlier in the more dangerous habitat. Harfenist & Ydenberg (1995) observed a similar predation risk effect on provisioning behaviour in rhinoceros auklets. Owing to our imprecise technique to infer parental provisioning in this study, we may have had insufficient power to detect a weak effect of predation risk.

The accumulation of extensive fat deposits by young seabirds may be inevitable when the provisioning diet is high in energy but low in protein content (Thomas 1984; Thomas et al. 1993), or it may serve an adaptive function. Parents may provide young offspring with extra reserves (sometimes termed 'overfeeding') to subsidize energy demands of nestlings late in the nestling period (Ricklefs & Schew 1994), reduce the probability of nestling starvation when foraging success is stochastic (Ricklefs & Schew 1994), buffer nestlings in the event of unpredictable food delivery (Lack 1968; Ricklefs et al. 1980) or parental mortality (Clark & Ydenberg 1990), or supply a nutrient that is scarce (Taylor & Konarzewski 1989, 1992).

In the early literature on seabird breeding behaviour, it was implied that mass recession was a necessary consequence of having acquired surplus fat (Lack 1968), but hypotheses for fat accumulation do not explain why nestlings lose some of the surplus fat before fledging. The proximate mechanisms of mass loss are well understood at least in some species and include metabolism of fat reserves or water loss during tissue maturation (Ricklefs 1968; Thomas et al. 1993). Mass loss also may be accompanied by a reduction in parental provisioning, and indeed, this is often assumed. Constraints on development or wingloading sometimes are invoked to help explain why prefledging mass recession occurs. For example, according to the 'wingloading hypothesis', losing surplus fat and thus lowering the wing area to body mass ratio is necessary for flight or diving following nest departure (cf. Ricklefs 1968; Pennycuick 1972; Martins 1997).

We reject the wingloading hypothesis and the other alternative hypotheses presented in the Introduction. None of the three predictions of the wingloading hypothesis was upheld, suggesting that Cassin's auklet nestlings do not fledge according to some simple rule about flight readiness. If nestlings required a longer period of structural development to ensure postdeparture survival than provided by parents, nestlings should consider only their own developmental state in their departure decisions. However, our data show that nestlings considered parental behaviour, namely recent feeding history, in addition to their developmental state (i.e. their mass and age). The flexible timing hypothesis does not predict that nestling departure decisions depend on nestling mass, age, or parental provisioning, and therefore on its own is insufficient to account for our observations. Finally, the idea that overfed nestlings would take advantage of the safety of the burrow until reaching an optimal fledging mass is insufficient because nestlings considered recent feeding history and their age in their departure decisions.

According to the theory we develop here, the parents' and chick's assessments of the costs and benefits interact to produce prefledging mass recession. We suggest that irregular provisioning and nest safety from the nestling's perspective are two important features contributing to mass recession in Cassin's auklets and perhaps other seabird species. Seabird nestlings generally are protected from predators, so remaining in the nest does not pose additional predation risk. Irregular provisioning due to stochastic foraging success or extended provisioning trips is common, and the evidence to date suggests that provisioning becomes increasingly infrequent with nestling age. Furthermore, mass recession may be exagerrated in Cassin's auklets at Triangle Island because colony visitation by adults and nestling departure only occur during the night. Unfed nestlings that gamble on future provisioning must wait at least until the following night when fledging is again possible.

Once parental provisioning and nestling departure decisions are better understood, predictions can be generated about the amount of mass recession expected between years or between colonies that differ in mortality and growth rate regimes. Further studies using real data on parental provisioning rates are required to determine how nestling condition influences parental provisioning. Exchanging nestlings of different sizes and ages and observing parental reaction also may help elucidate the nature of provisioning decisions. Supplementary provisioning studies may be useful for assessing whether or not nestlings consider preceding growth in their departure decisions. Owing to the complex interaction between parental provisioning and nestling departure decisions, simulation models may help to generate predictions about the expected intensity of prefledging mass recession. Finally, colony-specific measures of mortality and growth rates at the breeding site and at sea would be required for comparative studies.

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