

Precocial nest departure in the Alcidae

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ABSTRACT

The avian family Alcidae is unique among birds in having species with widely divergent developmental modes. In all alcids, the juvenile phase is composed of a period spent in the nest and a subsequent period at sea completing growth; the age at transition varies greatly between species. Previously, semi-precocial (species completing more than half of growth in the nest before departure to the sea) and intermediate (one-quarter to one-third of growth) alcid species have been modelled. Here a model is developed to investigate selective factors favouring the evolution of precocial nest departure in the Ancient Murrelet *Synthliboramphus antiquus*. The fitness-maximizing age to make the transition from nest to sea (nest departure) is calculated under various assumptions, for both parents and offspring. The model shows that the potential for growth at sea following nest departure is the strongest factor influencing the age at departure. A second important factor is the danger posed by predators to provisioning parents, while the two-egg clutch of murrelets (most other alcids lay a single egg) is less important. There is a small region of the parameter space (with high ocean growth and dangerous provisioning) within which precocial nest departure is favoured from the point of view of both parents and offspring. The zone of conflict between parents and offspring is also narrow. These results are evaluated with respect to the precocity hypothesis of Gaston.

Keywords: alcid nest departure, Ancient Murrelet, growth–mortality trade-off, parent–offspring conflict, precocity.

INTRODUCTION

The widest range in developmental pattern observed in any avian family exists in the Alcidae (auks, puffins and relatives). Fifteen of the 22 living species are ‘semi-precocial’, growing to 50% or more of final adult body mass on food provisioned to the nest by their parents. Fledglings are usually independent of their parents, but in the Dovekie (*Alle alle*) they are cared for by the male parent. The three ‘intermediate’ species grow to about 25% of adult body mass in the nest, whereupon they depart to complete their development at sea under the care of one parent, again usually the father. Species in both these groups have been widely studied (e.g. Nettleship and Birkhead, 1985). Less well-known are species in the genus *Synthliboramphus*, which depart the nest as 1- or 2-day-old downy chicks, a trait termed ‘precocity’. Both parents tend the chicks at sea. Comparative studies have indicated

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that the ancestral condition is semi-precocial, with derived intermediate and precocial modes. DNA phylogenies (Moum *et al.*, 1994; Friesen *et al.*, 1996) are consistent with this, although they are as yet unable to resolve the tree completely at one important node. All species with post-departure parental care occur above this node, but their exact relationships remain unclear.

In previous papers, my colleagues and I presented models that examine the evolutionary factors shaping the semi-precocial and intermediate modes (Ydenberg, 1989; Clark and Ydenberg, 1990a,b; Ydenberg *et al.*, 1995). These papers use the following framework: the juvenile life history is composed of two phases, nest and ocean, that are successively occupied by the growing chick. Both phases have associated growth and mortality characteristics, and the models calculate the nest departure (i.e. transition from nest to ocean phase) age and mass that maximizes fitness. Provisioning the nest may pose a danger to the parent from predators. In this paper, I use this framework to analyse the selective forces favouring precocial nest departure.

The most complete study of a precocial alcid is that on the Ancient Murrelet *Synthliboramphus antiquus* by Gaston (1992). Gaston provides a valuable discussion on the evolution of precocity (see his Chapter 15; see also Gaston and Jones, 1997) which suggests that important factors involved are the brood size of two (most alcid species lay only a single egg) observed in this species and its congeners and, in particular, the risk of predation on provisioning parents. Later, I discuss the results obtained here with reference to Gaston's hypothesis.

THE MODEL

The model calculates the fitness (maximum expected lifetime reproductive success) of all possible nest departure ages ($t_d = 1, 2, 3 \dots 50$) under a variety of circumstances, seeking those that favour the precocial pattern observed in the *Synthliboramphus* murrelets. Fitness is calculated from the point of view of both parents and offspring. In what follows, I outline the model and the fitness calculation algorithm. All symbols and parameter values are given in Table 1.

Growth

Living Ancient Murrelet nestlings depart at 1 or 2 days of age, and parents never deliver food to the nest. Thus the model requires speculation about how ancestral murrelets would have performed as provisioners, using inferences based on data from related or ecologically similar species. Gaston (1992) summarizes the relevant natural history. In the model, parents can have broods of either one or two nestlings ($b = 1, 2$). It is reasonable to suppose that the offshore feeding and nocturnal provisioning habits of Ancient Murrelets would make it difficult to provision two nestlings; therefore, I assume that lone nestlings grow more rapidly than do pairs, as is observed in the closely related *Cephus* guillemots (Asbirk, 1979; Emms, 1987). At sea, however, the growth rate is assumed to be independent of brood size because the parents do not have to travel long distances between their chicks and the food supply. Very young Ancient Murrelet chicks have also been observed to feed themselves (see Gaston, 1992, p. 131).

Following Gaston (1992), I assume that the ancestral Ancient Murrelet was semi-precocial and hence must have grown in the nest before departure, as on the following trajectory:

$$G(t, b) = c_2 (1 - e^{-c_1 t}) + h \quad (1)$$

where $G(t, b)$ is the mass of a nestling in a brood of b on day t , h is the mass at hatch, c_2 is the asymptotic mass and c_1 is the growth rate constant. Both c_1 and c_2 are assumed to be lower when $b = 2$, so that if there were a nestling phase, the growth trajectories up to the day of nest departure would follow those illustrated in Fig. 1.

After nest departure on day t_d , nestlings grow at rate c_0 until the final day of the breeding period ($T = 50$ days). I treat c_0 as a parameter, varying it between 1 and 6 $\text{g} \cdot \text{day}^{-1}$. The mass on day t of a chick from a brood of size b , which left the nest on day t_d , is:

$$Y(t, t_d, b) = G(t_d, b) + c_0 \cdot (T - t_d - 1) \quad (2)$$

The ‘-1’ arises because no growth takes place at sea on the day of nest departure. Gaston (1992) found that parents and their chicks spent most of the first day swimming away from the nesting islands, presumably to feeding areas.

Survival

I assume that nestlings are at greater risk from predators at sea, so that their daily survival is greater on land ($s_n > s_s$). Gaston (1998) considers this critical assumption, especially as it pertains to intermediate alcid species. I also assume that provisioning nestlings is more dangerous than tending chicks at sea for the parents, so that their daily survival rate is lowered by provisioning visits to the nest ($s_r < s_l$). Survival of the parents from the end of one breeding season until the start of the next is denoted s_w . The probability that an offspring from a brood of size b and departing the nest on day t_d survives to breeding, assessed at hatch, is $S_0(t_d, b)$. A parent of a brood of b that departs on day t_d survives until the next breeding season with probability $S_p(t_d, b)$, also assessed at hatch.

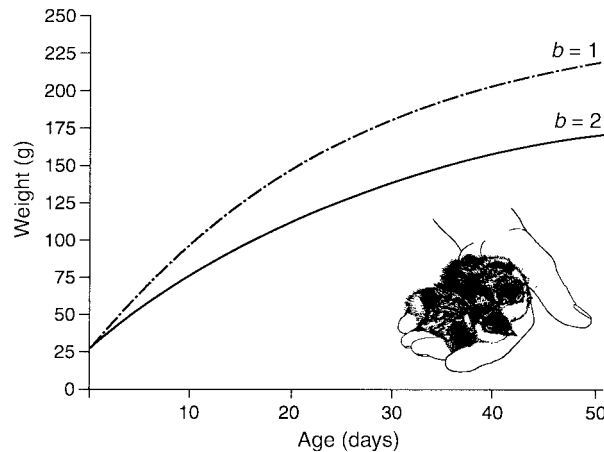


Fig. 1. The growth of Ancient Murrelets that would hypothetically be observed if they remained in the nest instead of departing to sea following hatch. The growth of broods of one (upper curve) is faster than that of broods of two (lower curve), as observed in the closely related Black and Pigeon Guillemots. The effect of reduced growth in broods of two on nest departure age is examined in Fig. 3.

I assume that chicks that attain a higher mass by day T have a higher probability of surviving until breeding age (see Ydenberg, 1989). Following Clark and Ydenberg (1990a), chicks with mass $y = Y(T, t_d, b)$ on day T survive to breed with probability Φ , where

$$\Phi(y) = \begin{cases} \gamma(y - y_{\text{crit}}) & \text{for } y > y_{\text{crit}} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

and y_{crit} is the minimum mass on day T required for survival.

Fitness characterization: Parents

I assume that parents behave to maximize expected lifetime reproductive success, denoted $R(t_d, b)$ to emphasize its dependence on t_d and b . $R(t_d, b)$ is equal to the product of the expected reproductive success from the current breeding season, $(b \cdot S_0(t_d, b))$, and the expected number of breeding seasons remaining. With the simplifying assumption that mortality is age-independent (cf. Tokuda and Seno, 1994), this is equal to $1/(1 - S_p(b, t_d))$, so that

$$R(t_d, b) = (b \cdot S_0(t_d, b)) / (1 - S_p(b, t_d)) \quad (4)$$

Thus, both current expected reproductive success and residual reproductive value depend on the parents' behaviour.

Fitness characterization: Offspring

In previous work, I assumed that offspring behave so as to maximize their expected survival to breeding age, $S_0(t_d, b)$, at which point they expect a lifetime reproductive success $R(t_d, b)$, and that their fitness can be expressed as the product of these terms. As pointed out by Godfray (1995), however, it is necessary to take account of the effect offspring behaviour will have on the survival prospects of parents. An earlier nest departure means that parents need to make fewer dangerous provisioning trips, but exposes the chicks to the hazards of the sea at an earlier age. Thus, this must be considered in an inclusive fitness context. The chick's inclusive fitness has three components: a change in fledging age alters the offspring's own fitness, that of its sib and that of the parent. Let t_d' indicate the nest departure age that maximizes $R(t_d, b) \cdot S_0(t_d, b)$. The change in parental fitness arising from a change in nest departure age from t_d' to t_d is

$$\Delta P = [(b \cdot S_0(t_d, b)) / (1 - S_p(t_d, b))] - [(b \cdot S_0(t_d', b)) / (1 - S_p(t_d', b))]$$

The change for both the nestling and its sib is

$$\Delta O = [S_0(t_d, b) - S_0(t_d', b)]$$

With coefficient of relatedness r , inclusive fitness $F(b)$ is

$$F(1) = r\Delta P + \Delta O \quad (5a)$$

when brood size is one ($b = 1$), and

$$F(2) = r\Delta P + (1 + r)\Delta O \quad (5b)$$

in broods of two ($b = 2$). In the calculations made here, $r = 0.5$. I assume that natural selection has adjusted offspring behaviour to maximize $F(b)$.

Fitness algorithm

To calculate fitness, $S_0(t_d, b)$ and $S_p(t_d, b)$ are computed for all values of t_d ($= 1, 2, 3 \dots 50$) under a set of parameter values and the results are inserted into equations (4) and (5). In making these computations, each day's events are assumed to occur with the following sequence: (1) nestling departs, if optimal; (2) parent provisions, if alive and optimal; (3) nestling departs, if not provisioned; (4) nestlings perish with appropriate probability. Thus, if a nestling dies, the parent does not discover this until the next night's provisioning visit.

If nest departure occurs on the first day ($t_d = 1$), then 0 days are spent in the nest and T days are spent at sea. According to the growth dynamics in equation (2), the chick(s) will have mass $Y(T, t_d, b)$ on day T . It will have had to survive T days at sea at daily survival rate s_s , and will survive from day T until breeding with probability $\Phi(Y(T; 1; b))$. Therefore,

$$S_0(1, b) = s_s^T \Phi(Y(T; 1; b)) \quad (6)$$

The parent spends T days at sea tending the nestling with daily survival rate s_t , and so

$$S_p(1, b) = s_t^T s_w \quad (7)$$

If nest departure occurs on the second day ($t_d = 2$), the nestling will spend 1 day in the nest with daily survival rate s_n and $T - 1$ days at sea with survival rate s_s . However, if the parent dies in period 1 and the nestling is not fed, it will depart and grow and survive according to equation (6). The latter occurs with probability $1 - s_f$ and the former with probability s_f . Thus

$$S_0(b, 2) = (1 - s_f) s_s^T \Phi(Y(T; 2; b)) + s_f s_n s_s^{T-1} \Phi(Y(T; 2; b)) \quad (8)$$

The parent spends $T - 1$ days at sea tending the nestling with daily survival rate s_t , and 1 day provisioning with survival s_f , and so

$$S_p(b, 2) = s_f s_p^{T-1} s_w \quad (9)$$

(As the parent would not, according to the assumptions, discover the death of a nestling until a visit on the following night, this possibility does not need to be taken into account until day 3. The daily survival at sea is assumed to be similar whether tending chicks or not.) The derivations are continued for $t_d = 3, 4, 5 \dots 50$. These quickly become very laborious, and the computations are actually made from recursion equations relating the successive days one to another (see also Clark and Ydenberg, 1990a). The fitness-maximizing departure age is found by comparing all values of $R(t_d, b)$ for parents and all values of $F(b)$ for offspring.

RESULTS

Four main factors were varied in making the computations: (1) the daily rate of ocean growth was varied from 1 to 6 g·day⁻¹; (2) parental provisioning was considered safe ($s_f = 0.9995$), dangerous ($s_f = 0.9900$) or very dangerous ($s_f = 0.95$); (3) the brood size was restricted to one ($b = 1$), or parents chose the brood size ($b = 1, 2$) that maximized their fitness ($b = b^*$); and (4) the post-departure daily survival of offspring was varied from 0.9995 to 0.98. These factors include those that Gaston (1992) considers in his hypothesis for precocity, the intent here being to examine how these factors interact when combined. All symbols and parameter values are given in Table 1. The parameter values used are based

Table 1. Parameter values used in the basic model

Symbol	Definition	Value
b	brood size	1, 2
c_1	rate constant in growth function G	-0.0413 ($b = 1$), -0.033 ($b = 2$)
c_2	asymptote in growth function G	220 ($b = 1$), 200 ($b = 2$)
c_0	ocean growth rate	$1 \dots 6 \text{ g} \cdot \text{day}^{-1}$
γ	fitness coefficient	0.005
$\Phi(y)$	probability of surviving to breed of nestling with mass on day T of y	$\gamma(y - y_{\text{crit}})$ for $y > y_{\text{crit}}$ 0 otherwise
$G(t, b)$	mass of nestling in brood of size b on day t	$G(t, b) = c_2 (1 - e^{c_1 t}) + h$
h	hatch mass	28 g
$R(t_d, b)$	expected lifetime reproductive success	
$S_0(t_d, b)$	probability offspring survives to breeding, assessed at hatch	
$S_p(t_d, b)$	probability parent survives to next breeding, assessed at hatch	
s_f	daily survival of provisioning parent	0.9995 (safe), 0.99 (dangerous), 0.95 (very dangerous)
s_n	daily survival of nestling	0.9955
s_s	daily survival of offspring at sea	0.9962 (also 0.999, 0.98 in Table 2)
s_t	daily survival of parents tending chicks at sea	0.9998
s_w	overwinter survival of adults	0.80
t	day in the breeding period	1, 2, 3 $\dots$ 50
t_d	nest departure day	
T	final day of breeding period	50
y	critical lower weight for offspring survival	170 g
$Y(t; t_d; b)$	weight on day t of nestling from brood of size b that departed on day t_d	$G(t_d, b) + c_0 \cdot (T - t_d - 1)$

on information given by Gaston (1992) where possible. Other values are those used by Clark and Ydenberg (1990a) in similar calculations for the Atlantic Puffin, but are little more than guesses. I examine the sensitivity of the model to these values below.

The effects of ocean growth rate and provisioning danger

The basic pattern seen in all the results is illustrated in Fig. 2A. Ocean growth rate has the strongest effect of all the parameters; as it increases from 1 to $6 \text{ g} \cdot \text{day}^{-1}$, the optimal nest departure age falls from 50 days to 1 day. Increasing the parental provisioning risk steepens the rate at which nest departure age falls with the ocean growth rate, so that a younger age of departure is chosen when it is more dangerous to provision, exactly as Gaston (1992) asserts in his hypothesis.

Parent-offspring conflict

The difference in the optimal departure age from the viewpoints of parents and offspring is also indicated in Fig. 2. Parental and offspring optima conflict by 0–5 days. When at risk,

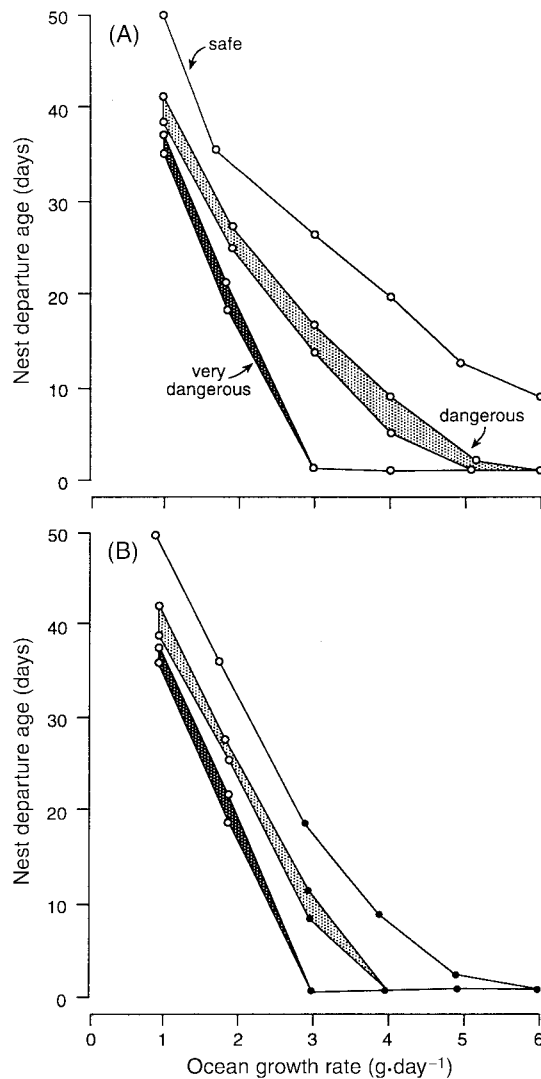


Fig. 2. The nest departure age chosen by Ancient Murrelet parents and offspring using the parameter values given in Table 1. Parental provisioning risk is considered safe ($s_f = 0.9995$), dangerous ($s_f = 0.99$) or very dangerous ($s_f = 0.95$), and both the parents' and offspring's choices are displayed. In (A) the brood size has been set at one ($b = 1$); in (B) the parent chooses the brood size (one or two) that maximizes its fitness ($b = b^*$). Open circles indicate that $b^* = 1$; solid circles indicate that $b^* = 2$. The shaded areas indicate the zones of parent-offspring conflict, with the upper boundary representing the offspring's and the lower boundary the parents' optima.

parents prefer a younger nest departure age than do the offspring, and the degree of conflict is greatest at intermediate (= 'dangerous' in Fig. 2) provisioning risk. The higher the provisioning risk, the broader the range of ocean growth rates under which both parents and offspring favour precocial nest departure.

The effect of brood size

In Fig. 2B, the model parent is able to choose the brood size (one or two) that maximizes fitness; the effect of this choice can be seen by comparing Figs 2B and 2A. The higher brood size is preferred whenever the ocean growth rate exceeds $2 \text{ g} \cdot \text{day}^{-1}$. The ability to raise a brood of two when optimal does lower the nest departure age under some circumstances, but the effect is small compared with those of ocean growth rate and parental risk.

The effect of the assumed slower nestling growth rate in broods of two is examined in Fig. 3. Without this assumption, model parents always choose a brood size of two and favour an older nest departure age.

Post-departure mortality of offspring

Gaston (1992, p. 219) states that, for his precocity hypothesis to work, the mortality of chicks after going to sea cannot be markedly greater than that suffered by young of other alcid species during the pre-fledgling period. The effect of post-departure mortality was investigated by varying s_s , the daily survival at sea. Lowering s_s from 0.999 to 0.98 lowers survival over 50 days from 0.951 to 0.364. The results are given in Table 2. When survival at sea becomes more precarious, the optimal age of nest departure rises from the points of view of both parents and offspring, narrowing the range over which precocity is favoured, as Gaston's hypothesis requires. However, at high rates of ocean growth, precocial nest departure is favoured by both parents and offspring, even if post-departure mortality is high.

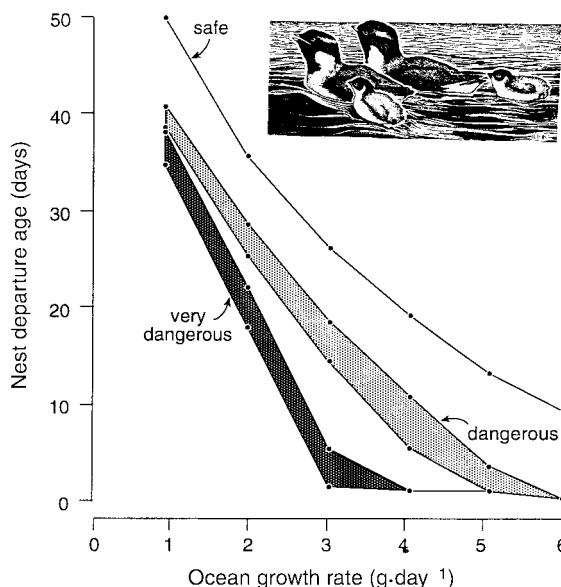


Fig. 3. The effect of removing the assumption that broods of two grow more slowly. Parameters identical to those used in Fig. 2B, except that nestlings in broods of two grow as rapidly as those in broods of one. In the absence of a growth penalty, the parent always chooses a brood size of two, and the nest departure age is higher. The shaded areas indicate the zones of parent-offspring conflict, with the upper boundary representing the offspring's and the lower boundary the parents' optima.

Table 2. The effect of post-departure survival of offspring on nest departure age under safe, dangerous and very dangerous provisioning

Ocean growth rate (g · day ⁻¹)	Nest departure age (days)								
	$s_s = 0.999$			$s_s = 0.9962$			$s_s = 0.98$		
	b^*	t^*_{P}	t^*_{N}	b^*	t^*_{P}	t^*_{N}	b^*	t^*_{P}	t^*_{N}
Safe provisioning ($s_f = 0.9995$)									
1	1	47	47	1	50	50	1	50	50
2	1	33	33	1	35	35	1	50	50
3	2	17	17	2	18	18	1	27	27
4	2	7	8	2	9	9	2	21	21
5	2	1	1	2	2	2	2	16	16
6	2	1	1	2	1	1	2	13	13
Dangerous provisioning ($s_f = 0.99$)									
1	1	36	38	1	38	41	1	50	50
2	1	23	26	1	25	27	1	40	44
3	2	7	10	2	8	11	2	15	18
4	2	1	1	2	1	1	2	1	5
5	2	1	1	2	1	1	2	1	1
6	2	1	1	2	1	1	2	1	1
Very dangerous provisioning ($s_f = 0.95$)									
1	1	33	35	1	35	37	1	50	50
2	1	17	20	1	18	21	1	30	35
3	2	1	1	2	1	1	2	1	1
4	2	1	1	2	1	1	2	1	1
5	2	1	1	2	1	1	2	1	1
6	2	1	1	2	1	1	2	1	1

Note: Parameter values are given in Table 1; s_s is the daily survival at sea following nest departure. Reducing s_s from 0.995 to 0.98 reduces survival over 50 days at sea from 0.605 to 0.364. t^*_{P} indicates the optimal nest departure age from the parents' point of view, while t^*_{N} indicates that from the offspring's viewpoint. b^* is the brood size that maximizes parental fitness.

The effect of adult overwintering survival

To establish the influence of adult survival on the nest departure ages chosen, adult overwinter survival was raised from 0.80 to 0.95. The effect is to reduce somewhat the nest departure age, which is to be expected, because raising overwinter survival increases the value of the future for parent Ancient Murrelets, and hence makes them more reluctant provisioners.

DISCUSSION

The results of the model developed here show a small region of the parameter space in which precocial nest departure is favoured by both parent and nestling Ancient Murrelets.

The factors favouring precocity include high growth rate at sea of the offspring and danger to the provisioning parent. Gaston's (1992) precociality hypothesis explicitly identifies the latter, but does not consider the former directly, although he argues (p. 216) that the existence of precocity suggests that food at sea is predictable, rather than ephemeral as Sealy (1973) previously inferred, because parents with chicks that cannot fly would be greatly hampered in locating and exploiting unpredictable patches of prey.

Gaston (1992, p. 217) also considers the idea, advanced by some authors (e.g. Sealy, 1973), that the brood of two of the *Synthliboramphus* murrelets and precocity evolved in response to the difficulty of provisioning nestlings. As he points out, it appears that most seabirds evolved single-egg clutches in response to difficult or slow provisioning, and it is not clear why Ancient Murrelets would have retained two nestlings (the ancestral condition) and evolved precocity instead. The results obtained here suggest that the brood size of two could be a consequence rather than a cause of precocity, because once precocity is favoured, parents taking two chicks to sea have higher fitness than those taking only one chick. Gaston and Jones (1997) suggest it is conceivable that more than two chicks could be reared if alcids had the ability to lay a larger clutch.

The model also shows that parent-offspring conflict over the timing of nest departure is not inevitable, as has been implied previously (Ydenberg, 1989; Clark and Ydenberg, 1990a,b). The existence of conflict does depend on parental provisioning danger, and is reduced or eliminated when provisioning is safe. Note that possible resolutions of the conflict that could affect fitness are not considered in the 'battleground' (*sensu* Godfray, 1995) models developed here.

Like any model, the present one merely illuminates the logical outcome of a set of assumptions, in this case demonstrating how factors whose importance is suggested by a study of natural history could interact to select for precocity. The sensitivity analyses illustrate the range over which each of the relevant parameters exerts influence and, to this extent, the implications of the model are clear. More troublesome are the possible effects of certain assumptions made to simplify the calculations. For example, the parents are treated as a single actor, whose potential deaths are not considered separately. Although these assumptions helped make the calculations tractable, their absence of course means that their potential consequences could not be evaluated.

Work along several lines of enquiry will be necessary to advance our understanding of nest departure strategies in general and precocity in particular (Ydenberg, 1998). Thanks to Gaston's (1992) study, the Ancient Murrelet is the best-known precocial alcid, but field studies of its three precocial congeners are required to improve our knowledge of murrelet biology. A complete phylogeny will also be essential; in particular, better resolution is needed to clear up the basal polytomy in the murrelet lineage (Moum *et al.*, 1994; Friesen *et al.*, 1996).

Alcid phylogeny and the natural history knowledge detailed in Gaston's (1992) discussion both suggest the evolution of precocity from a semi-precocial ancestor. Presumably, natural selection acted on heritable variation in the age of nest departure, driving it downward until full precocity was attained. Post-departure parental care must have evolved simultaneously; understanding its evolution is critical (A.J. Gaston, personal communication). Unfortunately, little is known about this difficult-to-study phase of alcids' lives. Post-departure care of offspring is found in all three intermediate species, and among semi-precocial alcids, in the Dovekie. Although the exact phylogeny is obscured by the basal polytomy referred to above, these species are closely related to the murrelets and it is

plausible that some degree of post-departure care is the ancestral state in this clade. If so, earlier departure could evolve under selection (by the factors described in this paper), accompanied by earlier initiation of post-departure care at sea by the parents, leading eventually to full precocity with the broad suite of adaptations discussed by Gaston (1992). The other possibility is that *Synthliboramphus* murrelets evolved post-departure care at sea independently of their close relatives. As it stands, there is little evidence for or against either of these alternatives.

Although developed specifically for Ancient Murrelets, the present model provides a general account of variation in nest departure age in the Alcidae as a whole, demonstrating how the factors presumed to be important in the evolution of nest departure age interact to select for an optimal nest departure age. These factors include the relative growth and mortality in the nest and at sea, the danger parents encounter in provisioning the nest, parent-offspring conflict and brood size variation. Depending on their magnitudes, the interactions of these factors select for nest departure ages that span the range observed in the Alcidae, from semi- to full precocity. Overall, the specifications of the model appear to be broadly consistent with what is known of alcid natural history, but more empirical testing is required before general conclusions can be drawn.

I calculated (under a set of assumptions, of course) the optimal balance between pre- and post-nest departure parental care from the point of view of both parents and offspring, but any of a host of other presumed important life-history attributes and trade-offs could be studied. The advantage of this numerical method is not that it gives detailed quantitative predictions (these often depend on unknown parameter values and hence must be suspect), but that it is easily adapted to other situations. For example, a model that asked questions about the duration of parental care among shorebirds would require only modest changes to what has been developed here, providing a way to explore and understand the complex interactions that are possible when several life-history variables interact.

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