Commentaries

Modeling Departure Strategies in Auks

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The family Alcidae is unique among birds in the amount of variation in nestling growth strategies exhibited (Sealy 1973, Gaston 1985). Chicks of some species depart the nest while only partially grown, a strategy that has been viewed as a consequence of constraints on the provisioning ability of the parents (Lack 1968, Sealy 1973, Birkhead 1977). Recently, Ydenberg (1989) and Ydenberg et al. (1995) have developed an explicit model (hereafter "the model") to describe factors affecting the decision of a nestling alcid to depart from the nest site. The model provides predictions that make a good fit with empirical observations that otherwise are difficult to explain. The apparent accuracy of these predictions might be considered a compelling argument for the validity of the model itself. Some mathematical weaknesses of the original model were detected by Byrd et al. (1991). Here, I would like to draw attention to cases that contradict one of the major assumptions used and which, if not answerable, indicate that the fit between predictions and observations may be a mere fluke.

Fundamentally, the model rests on two assumptions: (1) nestlings are safer in the nest than at sea ($u_n < u_o$, where u_n is the mortality rate in the nest and u_o the mortality rate at sea); and (2) the potential growth rate of the nestlings differs between the breeding site and the sea. This relationship varies with chick age. If the first assumption is violated, the model makes no sensible predictions (R. Ydenberg pers. comm.) because under such conditions, the model predicts that all chicks should leave immediately after hatching, which is a strategy adopted by very few species of seabirds (only murrelets in the genus *Synthliboramphus*; Lack 1968).

In its original formulation (Ydenberg 1989), the model was applied principally to the departure strategy of murres (*Uria* spp.), which leave the nest site when they are less than one-third grown and receive continued parental care at sea for about six weeks after departure. In the more recent version (Ydenberg et al. 1995), the model is applied to semiprecocial auks, exemplified by the Rhinoceros Auklet (*Ceror-*

hinca monocerata), a member of the tribe Fraterculini (Strauch 1985), among which the chick leaves the burrow at about 60% of adult mass and there is no parental care after departure. The most critical assumption of the model is the direction of the inequality in mortality rates (Ydenberg et al. 1995).

In their sample calculation, Ydenberg et al. (1995) estimate u_n as 0.0003 day^{-1}, based on the survival of chicks from hatching to fledging in Harfenist's (1991) study of Rhinoceros Auklets at Pine Island. The unmeasured variable u_0 was assigned arbitrarily as 0.02 day^{-1}, giving a survival probability over the 45-day time horizon of the model of 0.40. The value chosen for mortality at the breeding site is extremely low for a semiprecocial alcid in the Fraterculini. The average fledging success (chicks fledged as a proportion of those hatched) in 26 studies of Tufted Puffins (*Fratercula cirrhata*) was 0.71 ± SD of 0.23 (range 0.02 to 1.0) and in 17 studies of Horned Puffins (*F. corniculata*) 0.75 ± 0.14 (range 0.36 to 0.91). Fledging success in 10 studies of Rhinoceros Auklets (excluding Harfenist's) averaged 0.81 ± 0.10 (range 0.65 to 0.94; Byrd et al. 1993). These figures suggest that the survival of nestling Rhinoceros Auklets tends to be higher than that of other closely related auks, but that the survival figures obtained by Harfenist and used by Ydenberg et al. (1995) were unusually high, even for Rhinoceros Auklets. Using the mean figure for Rhinoceros Auklet from Byrd et al. (1993) and assuming the same duration of the nestling period (55 days) yields a daily mortality of 0.0034, which is an order of magnitude higher than the figure used by Ydenberg et al. (1995) but similar to the figure for Atlantic Puffins (*F. arctica*) cited by Ydenberg (1989). The highest value cited by Byrd et al. (1993) gives u_n as 0.0011 day^{-1}, still three times the value used by Ydenberg et al. (1995).

Turning to survival at sea, there is almost no information on the survival of Fraterculini during the immediate postfledging period, and none at all for the Rhinoceros Auklet. Estimates of survival to age of first breeding are available for the Atlantic Puffin, suggesting a mean annual survival of 0.80 (i.e. $u_o = 0.006$ day^{-1}). However, Ydenberg (1989) assumed that young puffins achieve adult survival (0.94; Har-

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ris 1984) by the end of their first year, making annual survival during the first year 0.32, and $u_o = 0.0030$ day^{-1}. This estimate is lower than the estimated mortality at the breeding site, based on the mean for values given by Byrd et al. (1993). However, all of the parameter estimates involved are likely to be very imprecise, so we cannot place too much reliance on this comparison. Ydenberg (1989) argued that the average mortality over the entire nestling period was an inappropriate measure, because most young alcids experience higher mortality during the first 10 days after hatching than later on. However, in the case of puffins, older chicks sometimes wander to the mouth of the burrow during the day, exposing themselves to the risk of predation by gulls (Nettleship 1972, Harris 1984). Hence, mortality also may increase just before fledging.

If, as Ydenberg (1989) implies, the mortality of fledgling alcids is largely a consequence of inexperience, and if the necessary experience can be acquired only after leaving the breeding site, then we cannot use their survival at this stage as a measure of the normal risk inherent in the marine environment. Instead, their low survival just after fledging must be seen as an inevitable cost of the transition from land to sea, and hence neutral to the outcome of the model. Ydenberg (1989) made provisions for such a transition cost in his first version of the model, although the estimates of u_n and u_o were not adjusted accordingly. The value of u_o assumed by Ydenberg et al. (1995), if it were realistic, could only represent a transition cost, because if prolonged for the whole of the first year it would give an annual survival of less than 0.01, and the population would soon be extinct. Once they have acquired the necessary experience, young puffins presumably have similar survival to that of breeding-age adults (as Ydenberg assumes for birds >1 year old). Under this assumption, the appropriate value for u_o is less than 0.0002 day^{-1}, below even the low value of u_n given by Ydenberg et al. (1995).

The case of the Thick-billed Murre (*Uria lomvia*), dealt with by Ydenberg (1989), can be examined in detail, because all of the relevant variables are known for a single colony at Coats Island, northern Hudson Bay (Gaston et al. 1994, unpubl. data). Terminal chick mortality rate (i.e. survival in the last week before departure) is 0.003 day^{-1}. Survival to three years is 0.45, and annual adult survival is 0.89. If we accept the argument that birds achieve adult survival after one year, this suggests a survival probability during the first year of 0.568. However, Gilchrist and Gaston (1997) showed that there is a 20% mortality of chicks at the time of colony departure, and when this is incorporated, u_o is estimated at 0.0009 day^{-1}, which is substantially lower than the terminal chick mortality rate. If we use the argument proposed above that the appropriate value of u_o is equal to the adult survival rate, this value becomes 0.0003 day^{-1}.

Further discussion of the point at which to measure u_o or the exact magnitude of appropriate values, probably is not profitable. Clearly, there will be risks inherent in the nest-departure process that are one-time costs of becoming independent. Some may apply during the late nestling period, as well as to the period immediately after fledging. These risks have not been measured, and it will be very hard (perhaps, in practical terms, impossible) to do so. In the current state of our knowledge of auk demography, any parameter values are likely to have very broad confidence limits, causing the predictions of the model to be similarly imprecise. As I have shown above, on the basis of current information, the most critical assumption of the model ($u_n < u_o$) appears unlikely to hold in many instances. However, and more important, u_o cannot be used at all until we can resolve the question of when it can be appropriately measured, or what proportion of mortality immediately postfledging should be treated as a cost of transition.

Notwithstanding the success of certain predictions of the model, unless the fundamental assumption that chicks are safer in their breeding site than on the sea can be verified, the model should be treated as a hypothetical demonstration of how departure decisions might be made by nestling alcids, rather than as a description of actual demonstrated processes. Further definition of u_o, and further explorations of the model's robustness to variability in input parameters (especially those relating to daily mortality rates in the nest and at sea), would be desirable before more elaborations of the model, or its predictions, are made.

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Evaluating Models of Departure Strategies in Alcids

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How should models in ecology be evaluated? Gaston (1998) charges that the "good fit with empirical observations that otherwise are difficult to explain" of alcid nest-departure models put forth in Ydenberg (1989) and Ydenberg et al. (1995) "may be a mere fluke." Although perhaps an uncharitable view, it is, of course, a possibility, and it reminds us that models should never be too readily accepted, even when they enjoy apparent success. They need to be subjected to repeated and rigorous testing in a variety of circumstances.

In his commentary, Gaston (1998) investigates the quantitative evidence for and against one of the model's key assumptions. I welcome and applaud this scrutiny, and I agree that the quantitative case here is far from closed. I acknowledge that issues of how and when to measure some of the input parameters need to be resolved, and I agree that the model's robustness to input variability should be explored. More data are also needed, although gathering them likely will be a lengthy process given the realities of the field work required. Few researchers have been

as dedicated to this slow and difficult work, or as successful, as has Gaston himself.

I would assert, however, that the most immediate value of these models has been overlooked among the doubts that Gaston raises: these models have helped identify new questions to ask, new and quantitative hypotheses to test, and a new view of life-history evolution in the Alcidae. Any reader who feels this is an audacious claim should peruse accounts of the Alcidae such as *The Thick-billed Murres of Prince Leopold Island* (Gaston and Nettleship 1981), *The Puffin* (Harris 1984), or *The Atlantic Alcidae* (Nettleship and Birkhead 1985). These authoritative references will reveal that prior to the publication of the first nest-departure model in 1989, mortality rates after nest departure hardly had been considered at all, and certainly not as a potentially critical factor in the evolution of the diverse departure strategies observed among species of alcids. No previous hypothesis about this diversity synthesized such diverse aspects of alcid ecology, emphasized the importance of intraspecific variation, or showed how the well-known seasonal decline in fledging mass or the pre-fledging mass recession observed in many species may be related phenomena. Not to claim too much, I hasten to point out that these predictions were de-

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