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## Modeling the Breeding Cycle of Long-lived Birds: Why Do King Penguins Try to Breed Late?

ANDERS BRODIN,<sup>1,4</sup> OLOF OLSSON,<sup>2</sup> AND COLIN W. CLARK<sup>3</sup>

<sup>1</sup>Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden;

<sup>2</sup>Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden, and  
British Antarctic Survey, Madingley Road, Cambridge CB3 0ET, United Kingdom; and

<sup>3</sup>Institute of Applied Mathematics, University of British Columbia, Vancouver, British Columbia V6T 1Z2, Canada

In life-history theory, an age-based approach traditionally has been used to predict how animals should optimize lifetime reproductive success (e.g. Charlesworth 1994). In this approach, animals are assigned to age classes, and individuals within an age class typically are considered as equivalent in condition, dominance status, quality, etc. Recently, McNamara and Houston (1996) argued that a state-based approach is more realistic to analyze decisions when animals differ in condition. Relevant states to consider may then be factors that affect an animal's size and condition, such as fat deposits, territory size, etc.

In this paper, we consider the tradeoff between parental survival and production of offspring for a long-lived species of bird. When breeding is costly, high parental effort in one season may affect the parent's condition in the subsequent breeding season (e.g. Gustafsson et al. 1994). We do not specify which states (fat deposits, feather condition, etc.) may be negatively affected by a high parental effort, but we assume that this negative effect ultimately is expressed in future survival. We simplify the parent's state to be its current breeding status, e.g. breeding or not breeding, and, if breeding, whether the chick is still alive. Our approach is general and will show how much reduction in future survival a parent can tolerate once the decision is made to breed. The simplicity of our approach makes an analytical solution possible; including more details (e.g. short-term changes in parental fat deposits) would require computer iterations.

When parental survival is independent of age, we will show that we can disregard the parent's age with respect to future parental lifetime reproductive success. The technique of dynamic modeling (Mangel and Clark 1988) makes it possible to relate an animal's present state to possible states at other times. In this way, costs and prospects for successful breeding in the current season can be weighed against future reproductive success. Here, we apply this method to a species with an interesting and unusual breeding cycle, the King Penguin (*Aptenodytes patagonicus*). We note, however, that

the method can be applied to any long-lived species in order to compare different breeding strategies.

Nonannual breeding in birds is restricted mainly to tropical regions with weak fluctuations in food availability (e.g. Moreau 1950, Voous 1950, Snow and Snow 1964, Lavery et al. 1968). Most of these birds have a breeding cycle that is shorter than one year. In birds with a long offspring developmental period, breeding cycles that exceed one year also have been found in regions with seasonal fluctuations. In these species, the typical pattern is biennial breeding in synchrony with seasons (see Immelman 1971), with one exception, the King Penguin.

King Penguins breed on sub-Antarctic islands and feed pelagically in polar waters (Williams 1995). They have a unique breeding cycle that normally takes around 14 to 16 months to complete, including molt (Stonehouse 1960, Berrat 1976, Weimerskirch et al. 1992, Jouventin and Mauget 1996, Olsson 1996). The single chick overwinters by itself on land and is rarely or never fed during this time. Thus, winter is a critical period with high mortality among chicks (e.g. Chérel et al. 1987). Parental feeding is resumed in spring (September to October) for some months until the chick becomes independent. The parents can then molt and start a new breeding attempt. After a successful breeding attempt, a new breeding attempt will start considerably later than in the previous year.

The main prey of King Penguins, mesopelagic lanternfishes (*Myctophidae*; Olsson and North 1997), fluctuate seasonally in abundance, with low availability during winter (Adams and Klages 1987, Hindell 1988, Chérel et al. 1993). Thus, the unique breeding cycle appears to result from time-restricted access to food such that the cycle is too short for penguins to complete molt and breeding and at the same time produce a chick with good prospects of survival (Weimerskirch et al. 1992, Olsson 1996).

Although many King Penguins try to breed late in the year after a successful breeding attempt, no or very few individuals seem to succeed (Weimerskirch et al. 1992, van Heezik et al. 1994, Jouventin and Lagarde 1996, Olsson 1996). Some individuals refrain from this late attempt and postpone breeding until the following summer. In fact, the timing of such late attempts and the proportion of birds undertaking

<sup>4</sup> Present address: Department of Ecology, Division of Theoretical Ecology, Ecology Building, S-223 62 Lund, Sweden. E-mail: anders.brodin@teorekol.lu.se

them have been shown to vary with the availability of food (Olsson and Brodin 1997), indicating that it is a state-dependent decision. Both late breeders that fail and birds that refrain from late breeding will be able to breed early the following year with a high probability of success (Olsson 1996).

Breeding is costly in many birds, with high energetic demands both for the parent itself (e.g. Ricklefs 1974) and for the act of feeding the young. Parents also may face an increased risk of predation. If breeding is costly in King Penguins, and the chance of success in late breeding attempts is almost zero, it is difficult to see how such late attempts can be adaptive. Because most individuals nevertheless try to breed late (Weimerskirch et al. 1992, Jouventin and Lagarde 1996, Olsson and Brodin 1997), we believe that there must be some chance of raising these late chicks. In this paper, we show how a state-dependent approach can be used to relate the costs of breeding to the decision of whether or not to breed.

*Methods.*—Let  $x$  be the chick's state at the beginning of a new summer. This variable can assume three different values: (1)  $x = 0$  (no chick alive); (2)  $x = 1$  (chick from early breeding alive); or (3)  $x = 2$  (chick from late breeding alive). Define  $F_i(x)$  to be a parent's expected lifetime reproductive success (given  $x$ ) for strategy  $i$ . There are two possible strategies: (1)  $i = 1$ , start breeding if  $x = 0$ , refrain from breeding if  $x = 1$ ; and (2)  $i = 2$ , start early breeding if  $x = 0$ , start late breeding if  $x = 1$ , refrain from breeding if  $x = 2$ . If all attempts succeed, individuals using strategy 1 will breed each second year, and individuals using strategy 2 will breed two years out of three. We assume that parental survival is independent of age, which will make  $F_i(x)$  independent of age too. We also assume that all costs for the breeder eventually can be measured in parental mortality. To simplify, we assume that mortality occurs during winter and that all chicks that survive the winter will fledge. If all late breeding attempts fail for individuals using strategy 2, the egg-laying sequence over years will be identical for both strategies: 1, 0, 1, 0, 1, 0, etc. Because the costs of early breeding will be the same for both strategies, we do not include any such cost in the comparison of the strategies. By analogy, the potential extra parental mortality from breeding will not differ between strategies if the egg-laying sequence is identical. We also assume that parental mortality is the same for breeders and nonbreeders.

For strategy 1 (S1), the parent's lifetime reproductive success (given current state of  $x$ ) is then given by the dynamic programming (Houston et al. 1988, Mangel and Clark 1988) equations:

$$F_1(0) = \beta[\alpha F_1(1) + (1 - \alpha)F_1(0)] \quad \text{and} \quad (1)$$

$$F_1(1) = 1 + \beta F_1(0), \quad (2)$$

where  $\alpha$  = the probability of a successful early breeding attempt, and  $\beta$  = the probability that the

parent survives until the next breeding season. Equation 1 states that a parent with no chick in spring will lay an egg, survive until next spring with probability  $\beta$ , and then find a surviving chick with probability  $\alpha$  and no surviving chick with probability  $1 - \alpha$ . In the latter case, the bird will be back in the state  $x = 0$  and future fitness will again be  $F_1(0)$ . Equation 2 shows that if the parent has a surviving chick in spring, the fitness will increase by 1, and the future fitness will be the chance of survival over the next winter,  $\beta$ , times  $F_1(0)$ . Insertion of equation 2 in equation 1 gives:

$$F_1(0) = \frac{\alpha\beta}{1 - \alpha\beta^2 - \beta + \alpha\beta'} \quad (3)$$

which is the expected lifetime reproductive success for an individual using strategy 1.

For strategy 2 (S2) the parent's lifetime reproductive success (given  $x$ ) is in accordance with the equations above:

$$F_2(0) = \beta[\alpha F_2(1) + (1 - \alpha)F_2(0)], \quad (4)$$

$$F_2(1) = 1 + \beta[\delta F_2(2) + (1 - \delta)F_2(0)], \quad \text{and} \quad (5)$$

$$F_2(2) = 1 + \beta F_2(0), \quad (6)$$

where  $\alpha$  and  $\beta$  are as in strategy 1, and  $\delta$  is the probability of a successful late breeding attempt. Here, equation 4 is the same as equation 1. Equation 5 says that a parent that finds a surviving chick after winter will increase fitness by one, commence a late breeding attempt, and survive the next winter with probability  $\beta$ . It will then find a surviving chick from the second breeding with probability  $\delta$  and no surviving chick with probability  $1 - \delta$ . Equation 6 states that if a late chick survives the winter, the parent's fitness will increase by one and the chance of surviving the next winter will be  $\beta$ .

Insertion of equation 6 in equation 5 and then equation 5 in equation 4 gives:

$$F_2(0) = \frac{\alpha\beta(1 + \beta\delta)}{1 - \alpha\beta^2(1 - \delta) - (1 - \alpha)\beta - \alpha\beta^3\delta}. \quad (7)$$

So far, we have assumed that there is no extra cost associated with trying a late breeding attempt. However, if there is an additional cost of late breeding, this will make breeding costs different for the two strategies. A coefficient between 0 and 1,  $\epsilon$ , can be inserted in equation 5 so that  $\epsilon\beta$  is overwinter survival of late breeders (e.g. if the extra cost of late breeding is very small,  $\epsilon \approx 1$ ):

$$F_2(1) = 1 + \beta\epsilon[\delta F_2(2) + (1 - \delta)F_2(0)]. \quad (8)$$

Instead of equation 7, we then obtain:

$$F_2(0) = \frac{\alpha\beta + \alpha\beta^2\delta\epsilon}{1 - \alpha\beta^3\delta\epsilon - \alpha\beta^2\epsilon + \alpha\beta^2\delta\epsilon - \beta + \alpha\beta'} \quad (9)$$

which is the expected lifetime reproductive success for individuals using strategy 2. In equations 3 and 9, we have expressions for the two strategies that are possible to compare. Because we are interested in the case when strategy 2 is better than strategy 1, setting  $F_2(0) > F_1(0)$  makes it possible to solve for  $\delta$  and  $\epsilon$ :

$$\delta > \frac{\alpha\beta - \alpha\beta\epsilon}{\epsilon - \beta\epsilon} \quad (10)$$

and

$$\epsilon > \frac{\alpha\beta}{\delta - \beta\delta + \alpha\beta} \quad (11)$$

*Results and discussion.*—To investigate particular aspects of the breeding cycle, we need a more detailed dynamic model with parameters like predation risk, energy expenditure, etc., and several behavioral options. To investigate more general questions, like whether high costs of breeding can ever be tolerated, a simple model like the one we present is more adequate.

No successful late breedings were observed in a six-year study in a small colony of King Penguins at South Georgia (all early breedings also failed in two of these years; Olsson 1996, 1997). Moreover, studies from other breeding locations show the same pattern in that no (or very few) late breeding attempts are successful (Weimerskirch et al. 1992, van Heezik et al. 1994, Jouventin and Lagarde 1996). Unless late breeding attempts imply extra costs, fitness for individuals using strategy 2 (S2) will then be identical with that for individuals adopting strategy 1 (S1) if all late breedings fail. Because this is the worst-case scenario for S2 individuals, S2 will always be superior to S1 if there is any chance that a late breeding attempt will succeed.

Even if no successful late breeding attempts have been observed, this does not mean that these attempts always fail. Over longer time periods it has been shown that food availability may fluctuate; for example, the availability of the Antarctic krill (*Euphausia superba*) in the Southern Ocean (Croxall et al. 1988). No King Penguins in the South Georgia colony laid an egg later than early April (Olsson 1996), although food still seemed plentiful. Most other studies have reported that the latest attempts end even earlier than early April (Barrat 1976, Weimerskirch et al. 1992, van Heezik et al. 1994, Jouventin and Lagarde 1996).

Including late breeders, Weimerskirch et al. (1992) reported a fledging success of 40.9%, whereas Jouventin and Lagarde (1996) measured 45% for early breeders. In our colony, 44 of 70 (63%) early breeding pairs in 1992 and 1994 succeeded in fledging a chick. Hence, we consider 50% to be a reasonable average value for early breeding success. Parental survival between seasons has been reported to range from 0.907 to 0.952 (Weimerskirch et al. 1992) and from

0.93 to 0.94 (Olsson 1996) when food is very abundant (and somewhat lower when food is less abundant; Olsson et al. unpubl. data). We assume 0.9 to be a reasonable figure in a long-term perspective, including years with lower food availability. If we insert these values in equation 3 for strategy 1, we then get:  $F_1(0) = 3.10$ . Because there are two parents raising one chick, a lifetime reproductive success of 2.0 would result in population equilibrium if all individuals breed. However,  $\alpha$  is the probability that a chick survives until fledging, and mortality between fledging and first breeding is not included. Young and inexperienced birds may have higher mortality at sea than adults. If  $\alpha$  is redefined as "survival from egg until first breeding" and decreased to 0.3,  $F_1(0)$  becomes 2.12.

If we set the probability of a successful late breeding,  $\delta$ , for individuals using strategy 2 to 0.1 ( $\alpha = 0.5$  and  $\beta = 0.9$  as above),  $F_2(0)$  becomes 3.29, compared with 3.10 for strategy 1 above. Besides chick mortality, postfledging mortality also may occur before the first breeding, and  $\alpha$  should then be lower. In our colony, 47% of the fledged young returned to the colony within four years. This is a minimum estimate, because some young may return later or to other colonies. Also,  $\delta$  should probably be lower than 0.1 because very few successful late breedings have been reported. If  $\alpha$  is decreased to 0.3 and  $\delta$  is decreased to 0.05,  $F_2(0)$  becomes 2.20, compared with 2.12 for  $F_1(0)$ .

The parameter  $\epsilon$  decreases parental survival for individuals starting a late breeding instead of just maximizing survival until the next breeding season, and the extra cost for parents that attempt to breed late becomes  $1 - \epsilon$ . With equation 11, we can calculate maximum values of  $\epsilon$  depending on the other parameters. If the chance of raising a late chick to independence,  $\delta$ , is 0.1, and  $\alpha$  and  $\beta$  are still 0.5 and 0.9, respectively, then  $\epsilon$  must be higher than 0.978 for strategy 2 (attempting late breeding) to be the optimal strategy. Even if  $\delta$  is increased to 0.4,  $\epsilon$  must still be higher than 0.91. Thus, King Penguins can tolerate only very small extra costs associated with late breeding attempts, which agrees with our observations in the South Georgia colony where no such costs could be detected (Olsson 1996). Moreover, we observed no terrestrial predation attempts on adult King Penguins. Foraging trips may be very long (Jouventin et al. 1994, Olsson et al. unpubl. data), but unless the risk of predation is increased during these trips, the extra cost of breeding probably is low.

Equation 10 makes it possible to predict the minimum chance of successful late breeding as a function of the cost of late breeding for strategy 2 to be optimal. If the reduction in survival is very small,  $\epsilon = 0.99$ , then a chance of a successful late breeding of 0.045 or more is sufficient.

In conclusion, the extra cost for attempting to

breed when the probability of success is low must be very small for long-lived birds. Even a chance of raising a late chick to independence as high as 0.4 would make a reduction in parent survival of less than only 9% tolerable. If, on the other hand, the cost is negligible, then a breeding attempt is always worthwhile if there is any chance of success. For a long-lived bird, such a chance might occur at the rate of one extremely good year out of 20, or something like this.

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## Flight Without Horizon References in European Starlings

ROBERT G. MOYLE<sup>1</sup> AND FRANK H. HEPPNER

*Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA*

Many birds fly at night, or in conditions in which a horizon reference is obscured or missing (Berthold 1993). Nonmigratory species such as European Starlings (*Sturnus vulgaris*) will fly near their roosts in large flocks long after the sun has set (Eastwood 1967). Nocturnal migration and flocking after dusk occur under a variety of meteorological conditions, including fog and heavy cloud cover (Evans 1972, Elkins 1983). These behaviors suggest that for some bird species, visual references are not always necessary to maintain straight and level flight.

Radar studies (Griffin 1972) suggest that some birds can maintain straight and level flight under completely overcast conditions, but birds flying within clouds may produce erratic tracks, suggesting disorientation in the absence of visual cues. Able (1982) used a tracking radar to examine the behavior of nocturnal migrants under overcast conditions and concluded that overcast skies did not result in changes in flight behavior. However, he acknowledged that some degree of disorientation occurred when birds seemed to be flying within or between cloud layers.

Williams and Teal (1973) blindfolded individuals of six species of birds (Song Sparrow [*Melospiza melodia*], White-throated Sparrow [*Zonotrichia albicollis*], Dark-eyed Junco [*Junco hyemalis*], House Sparrow [*Passer domesticus*], Rock Dove [*Columba livia*], and Herring Gull [*Larus argentatus*]) to observe their flight in the absence of visual cues. One out of every six birds tested tried to fly upside down and crashed, and one-third of the birds dropped immediately to the ground, often using fluttering flight. Only Her-

ring Gulls seemed to be little affected by the blindfolds, and 10 gulls exhibited normal flight. However, 2 of the 13 gulls used in the experiment would not fly and had difficulty standing upright.

Two types of orientation might be affected if visual cues are removed from a flying bird. The first is primary orientation, which concerns the positioning of the organism in three-dimensional space with reference to a constant direction, such as the gravitational pull of the earth. Superimposed upon this primary orientation is secondary orientation, which relates to the organism's ability to maintain a directional heading across the earth (Fraenkel and Gunn 1940). A bird deprived of visual cues might find it difficult to maintain a compass heading or heading toward the roost, but it might also experience a breakdown of primary orientation and be unable to maintain straight and level flight.

Primary or positional orientation has been studied relatively little, especially with respect to flying organisms, although several authors have speculated on possible mechanisms (Delius and Vollrath 1973, Jander 1975, Schöne 1984). Slanted banks of clouds can cause a human pilot to unknowingly fly in a bank (Bending 1959, Gillingham and Wolfe 1986). If no visual horizon reference is available and the pilot is flying without instrumentation, the ability to keep the plane straight and level will be lost almost immediately, and a total loss of control and downward spiral or spin to the ground usually are the result (Spector 1967).

*Methods.*—We used a wind tunnel to examine the flight behavior of European Starlings under four different lighting conditions, ranging from normal indoor lighting to darkness. The flight area of the tunnel measured 0.91 m (length) × 0.58 m (height) × 0.58 m (width). The front of the flight area was a honeycomb mesh and the back was wire screen. The top, bottom, and both sides were constructed of clear

<sup>1</sup> Present address: Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803, USA.  
E-mail: rmoyle@unix1.sncc.lsu.edu