SECTION 7: MANAGEMENT AND CONSERVATION

Models of swan population dynamics and growth: a review

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A model of Mute Swan breeding success is developed which depends on the females' abilities to gain weight in early spring. It is parameterised with data from Groningen, Netherlands. The model predicts that many swans may be able to achieve similar annual cygnet production over a wide range of incubation periods, and that their actual behaviours might thus be appreciably constrained by factors formerly thought to be of minor importance. Sensitivity analysis suggests these predictions are robust to two critical but poorly known factors: weights of females in late winter; changes in food quality and availability during early spring. The implications of the model to additional aspects of Mute Swan ecology and to the migratory arctic breeding swans are discussed.

The papers presented at the Third International Swan Symposium showed wide variation in the complexity of numerical data on population numbers and processes and the sophistication of techniques used for their analysis. Very few summarised data as mathematical models to check the consistency of the various estimates. Our spoken paper presented a very brief review of classical models of exponential and logistic growth (see, eg. Odum 1971), age structured models as illustrated by Leslie Matrices (Leslie 1945. see also Jeffers 1978, Bacon 1991a). It went on to review models that made use of measurements of body size and weight to indicate condition and hence potential survival and reproductive success (eg. Lomnicki 1978, Bacon 1982, Csetenyi & Logofet 1989, Bacon 1991). Finally the paper developed a 'physiological' model of the body resources needed by breeding female Mute Swans, *Cygnus olor*, and the mechanisms which might thus limit their annual production. This written paper presents only the physiological model, as details of the others are readily available elsewhere.

The theme of the physiological model is that weight of Mute Swans (and probably other swan species too) can be used as an index of their body condition, especially when corrected for body size (Beekman 1991, Bacon *et al.* in prep., see also Reynolds 1972, Andersen-Harild 1981). Several papers on moult of Mute Swans indicate weight losses, implying swans on poor quality food cannot moult without losing weight (eg. Andersen-Harild 1981, Willey & Halla 1972, van Dijk & van Eerden 1991). It is clear that the high arctic breeding swans, like arctic breeding geese, are dependent upon stored body reserves for forming their full clutch (eg. Kondratiev 1991). This model is parameterised with values for a study of Mute Swan breeding by Beekman (1991), for an area of the Netherlands where Mute Swans in spring feed mainly on grass fields and in drainage ditches with aquatic vegetation (algae and *Lemna* spp.). In early spring Mute Swans may be more restricted by food quality and quantity than at other times of year. However, a main aim of the model is to assess the relative breeding successes that might result from different strategies. We emphasise that analysis of data (eg. Walter *et al* 1991) tells us what swans did; but such analysis may tell us little about the costs or benefits acruing to other strategies, had these been possible. We present what happened in the joint contexts of what is desirable for the swans but impossible for them to achieve and also of what is possible for the swans but desirable for them to avoid.

Methods

The model has three main components. First, a pay-off curve, of offspring raised varying with clutch size and date incubation started. Second, a set of breeding resource requirements for females in terms of body masses gained and lost

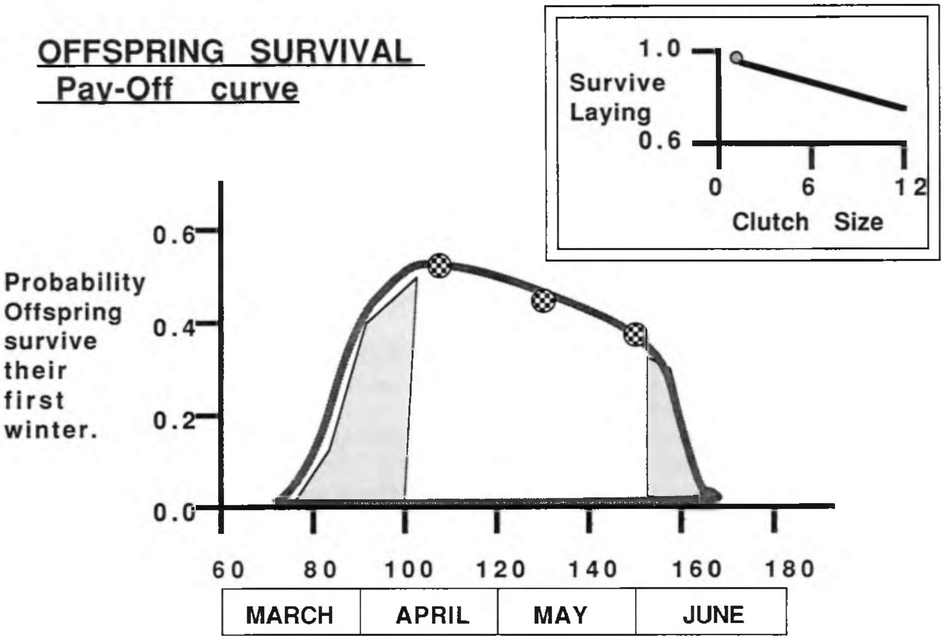

Fig 1. The probability that eggs will survive through their first winter to become indendent cygnets, depending on the date that their mother starts incubating the clutch (see text). Days are numbered from 1st January as day 1. The inset shows the probability that clutches of different sizes will survive from laying of the first egg to clutch completion and incubation.

during the season. Third, a set of estimated nutrition constraint curves, showing maximal (estimated) accumulation rates: these latter are only crudely known, but the qualitative predictions of the model seem quite robust to their uncertainty. The aim of the model is to take a pay-off curve (similar to the theoretical curves of Perrins 1970) and a set of plausible late-winter weights for breeding female Mute Swans near Groningen, and assess the likely consequences of differing restrictions on their ability to gain weight prior to egg-laying in spring. Such calculations elucidate females' 'best' breeding strategies given these constraints.

Offspring raised

Beekman's data record clutch loss during incubation as apparently constant with time (0.35 probability of loss during incubation). Survival between hatching and fledging increased (marginally significantly) with the date incubation started, whereas survival over the first winter decreased significantly with date. We have used his values to calculate three points on the pay-off curve (Fig. 1): the remainder of the curve has been invented to conform with known limits on observed dates of laying. The precise shape of the curve is not vital to the qualitative outcomes of interest.

The pay-offs of Fig. 1 are per egg per clutch for the (approximate) date on which incubation starts. The inset to Fig. 1 shows the decrease in probability that a larger clutch will survive laying, given an average interval between eggs of two days. When these two probabilities (for a given date and clutch size) are multiplied by each other and the clutch size they give the expectation of cygnets raised through their first winter. We emphasise that our dates refer to the start of incubation: incubation is more closely and usefully defined than the frequently-used 'date of first egg'. As a consequence our dates will be some two weeks later compared to 'first-egg' dates for average clutches.

Breeding resource requirements

Analysis of Beekman's data can be summarised as in Fig. 2. The female's body weight at first laying closely predicts her clutch size (approximately 350 gm of body mass being required for each egg). Incubating females begin incubation at weights close to 9.0 kg, and lose 63 gm/day during incubation. After hatching, females gain weight at a maximum of 80 gm day (note that

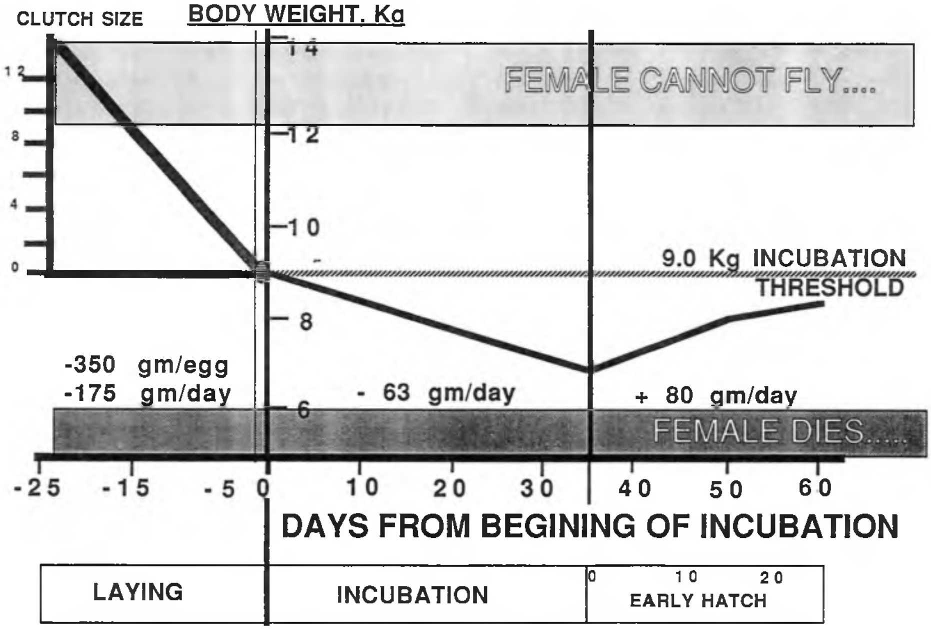

Fig 2. Average weight changes of female Mute Swans in the Groningen study area during different stages of the nesting cycle. The main axes show female body weights from 5.0 to 14.0 kg against time in days from the start of incubation. The threshold weight of 9.0 kg at which incubation starts is given as a horizontal line. The weight range between which females can fly and do not starve are indicated. A minor vertical axis indicates possible clutch sizes depending on female weight above 9.0 kg. Average weight changes of females are shown as a solid black line. Rates of change, in gm/day, are given below these lines.

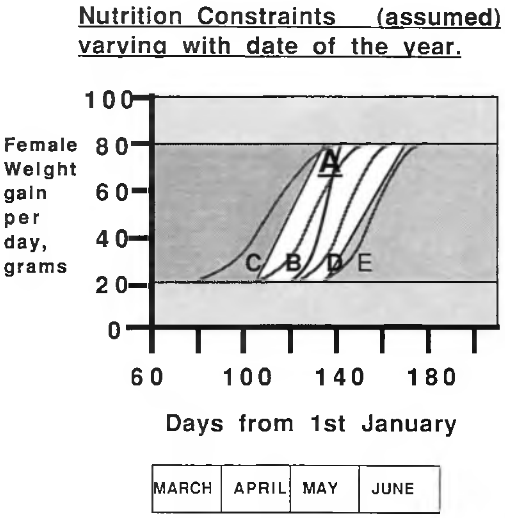

Fig. 3. Assumed rates of female body weight increase with date from 1 January. The horizontal lines at 80 and 20 gm/day are considered maximum and minimum rates. The solid curve A is that used in the model. The solid curves B and D gave realistic results: the dotted curves C and E produced unrealistic results. Accordingly it is suggested that a range of curves within the wide window of the unshaded region between 80 and 20 gm/day would all give realistic outcomes.

this is similar to the weight gains for growing cygnets). We note that likely ranges of female weights are 6.0 kg (just above lethal limit, c. 5.7 kg) to 13.0 kg (one kilo above weights at which females cannot fly, Beekman 1991). We take these average values as applying to all females. Beekman (in prep) shows that the relationships are closer if body weight is corrected for body size, but for simplicity our comments here refer to 'standard sized' females.

Nutrition constraints

We have a clear concept of resource intake being high in late spring and summer, and low in late winter and early spring, but little accurate data on its (average) change with season. Accordingly, we take the 80 gm/day increase in body weight by females post-hatching as being a maximum (Fig. 3). If gains during the whole winter were appreciably above 20 gm/day, then most swans could lay very large clutches: we take this as an approximate 'winter minimum' of nett accumulation (above maintenance requirements). We have little idea of the timing or rapidity of the change between the two levels, so the simulation model uses a wide variety of plausible curves (A-E in Fig. 3).

Estimated successes of different feasible strategies

The simulation model assumes a female may be of any weight between 6.0 and 13.0 kg (in 0.1 kg intervals) in late winter (day 60, taking 1 January as day 1). Given a particular starting weight the computer programme calculates her weight accumulation curve (following the constraints of Fig. 3 for one curve A-E), and for each possible clutch size (2 to 12) records the earliest date on which she could lay that clutch. Her expected rearing success is calculated from Fig. 2 for that date, and if her expected success is higher for a later date, the date for the highest later success and the expectation of offspring raised then are also recorded.

The estimated successes are shown in Fig. 4 as a 3D 'response surface' graph, with day-60 weight and clutch size (always on the optimal date for that clutch in those circumstances) predicting the expected number of offspring reared. Several interesting features are apparent. A planar surface in the bottom right (low weight, large clutch) indicates that low-weight females can only achieve large clutches too late for good rearing success. A planar surface at the back of the figure (high weight) indicates that heavy birds can always lay largish clutches at the best date. For many weights (8 to 10 kg) there is a steep decline in success for large clutches (that are achieved too late).

A surprising and important feature of the response surface is the lack of a clear 'optimum' for many weights. In the range 9 to 12 kg there is a pronounced flat 'shoulder' to the response surface, such that several clutches achieve very similar successes: indeed, for some starting weights the predicted success curve has two similar peaks. This implies that females may not have a clear optimal strategy, but a range of choices giving similar success. It is particularly important to note that the weight range for which we predict such a dilemma is not an extreme which would involve few breeders, but precisely the range likely to include most of the breeding females.

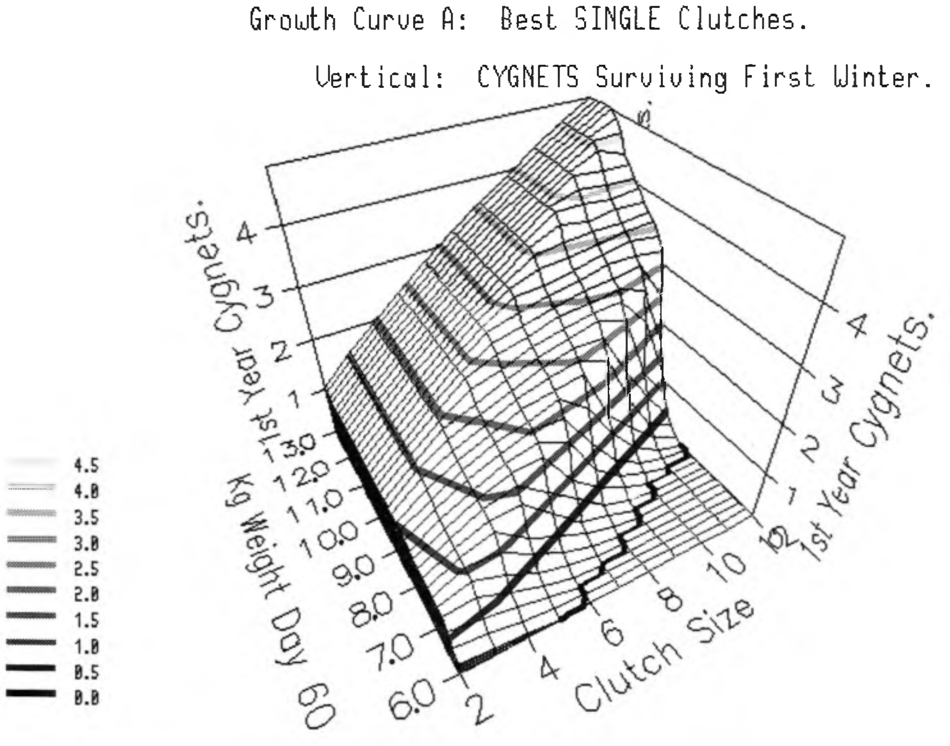

Fig. 4. The response surface of maximum number of cygnets surviving through their first winter, as predicted by the model depending on the late winter weight of their mother and the clutch sizes she could achieve given the growth constraints of Fig. 3A. The shaded contour lines show weights and clutches giving the same numbers of cygnets reared (see key for values of shaded lines). The hatched regions on the shoulder of the response surface indicate where females of a given starting weight can achieve similar cygnet production by either smaller earlier clutches or larger later ones. Note that these hatched regions coincide with the typical range of weights for adult females.

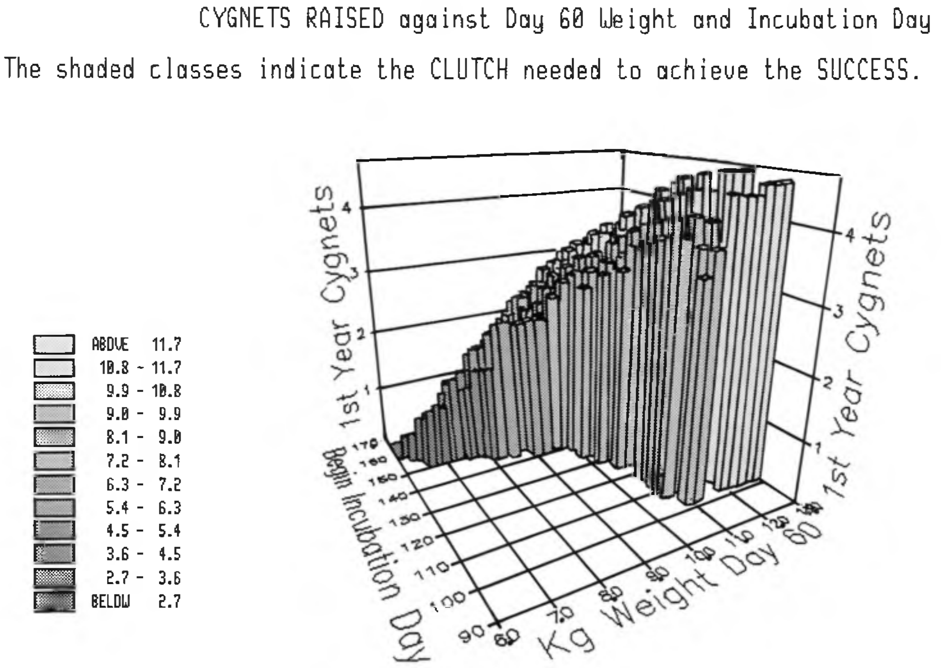

Fig. 5. This figure shows a partial response surface of cygnets surviving through their first winter. The area of the surface illustrated is restricted to that within 0.2 cygnets of the maximum achievable by a female of a given starting weight. Clutch sizes achieving the various successes are shown as columns with different densities of shading (see key). The multiple date columns for each female weight show the range of dates on which similar success (+- 0.2 cygnets) can be achieved.

Fig. 4 showed only the maximum success achieved by the optimal clutch size as constrained by starting weight. From that information alone it may seem rather arbitrary which of several similar strategies a female might adopt. However, if we look at the range of dates needed to obtain those optimal strategies for each clutch size (Fig. 5) a different picture emerges: the dates on which it is possible to achieve similar successes from the same clutch size can range from 5 to over 20 days (depending on the clutch size).

Fig. 5 shows the total range of starting weights (X axis) together with the sub-sets of combinations of incubation dates (Y axis) and clutch sizes (different column shadings) that achieve within 0.20 cygnets of the maximum success for a given female starting weight (the range of 0.2 is less than 10% of the maximum success for nearly all cases). If there was a single optimum strategy clearly better than all others for every weight then Fig. 5 would be a curve of single columns. It is apparent, however, that many similar, 'near optimal' successes occur over widely ranging dates for many starting weights. Hence other minor factors, not yet modelled, might cause a female to prefer the smaller clutches and earlier dates from such a range achieving similar successes.

A converse, but equally important, inference of Fig. 5 is that a clutch of a given size may be 'near-optimal' for some swans over a wide range of dates (depending on those swans' weights in late winter). If this is true then it would not be surprising that attempts to predict clutch size from laying date (eg. Bacon, 1980; Birkhead *et al.* 1983. Walter *et al.* 1991) do not explain much of the variance (30%). Those analyses were unable to incorporate the females' late winter weights as predictive factors. The present theoretical model suggests female weights may be crucial in constraining their feasible clutches. Given the constraint of their starting weights, then the optimal successes of females, and the dates and clutches which achieve them, may be inherently variable, as indicated in Fig. 5.

The results presented above were all derived using curve A of Fig. 3. Simulations were also run with curves B-E. In brief, the results from C suggest far too many low-weight females would breed, and the results from E that far too few high-weight females would breed. However, within the rather wide 'window' implied by curves B,A,D (unshaded portion of Fig. 3) the results reported above remain true. The overall magnitudes of achieved rearing successes change depending on the curves A-E, but the flat shoulder on the response surface persists, as does the wide range of dates needed by a female of a given weight to achieve similar high successes from different clutch sizes.

Replacement Clutches

The above predictions are based on the quite severe restrictions on the present model, and minor modifications to overall success might make big differences to the 'best' combination of clutch size and laying date. We briefly investigated one, the effect of replacement clutches. The sub-model for this assumes that every female begins incubating at a weight of 9.0 kg, and loses weight at 63 gm/day until the clutch is lost, which occurs with constant probability.

In order to lay a replacement clutch the bird must regain the lost weight plus enough reserves to lay a clutch, according to the dates of incubation start, clutch loss and the relevant nutrition constraint curve (Fig. 3). The best replacement strategy (date and clutch size) is calculated for each loss date, and the 35 possible 'bests' (one for each day of incubation) are averaged and discounted by the overall probability of needing a replacement (= losing the first clutch). The results are summarised in Fig. 6 as simple line graphs for the nutrition constraint curves A,B,D. Assuming most females start incubating between days 90 and 100, then they can expect an additional 0.2 to 0.4 cygnets surviving through the first winter from replacement clutches. As such replacement clutches are usually laid after the optimal date, their success declines steadily with season (Fig. 6): hence, other things being equal, the possibility of a repeat clutch should slightly favour early laying.

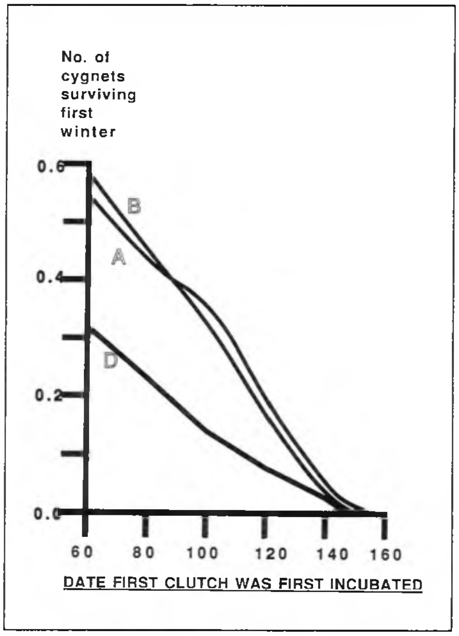

Fig. 6. Expected number of cygnets surviving through their first winter from the average replacement clutch, given the date the first clutch was first incubated and assuming the first clutch is lost on a random day during incubation. The three lettered response curves refer to successes achieved for the female body weight gain constraint curves of Fig. 3 having the same letter.

Accounting for replacement clutches in the simulation model confirms this expectation. The shoulder of the new response surface (as in Fig. 4) generally has a single peak corresponding to the earlier of the two peaks for the expectation from single clutches (Fig. 4). However, the magnitude of the effect of replacement clutches, while normally favouring early laying, does not remove the overall flatness of the shoulder region. Indeed, with the parameter values for Mute Swans in Groningen, the similarity between the two 3D figures is so close it is not worth printing both!

Discussion

If this 'nutrition constrained' model of breeding is realistic, it implies that factors formerly considered to be of secondary importance in determining a breeding strategy (here defined to be feasible combinations of clutch size and incubation date) might actually be crucial in determining which of several similar strategies was adopted. We will speculate about a few likely candidates.

Cygnet growth and survival

Cygnets' survivals through their first winter vary significantly with their autumn weights (Beekman 1987,1991, de Leeuw & Beekman 1991). Thus cygnets that hatch in time to benefit from a longer growing period, and perhaps the peak of the growing period, could have a crucial advantage. The shape of the cygnet growth curve is known for Beekman's study area in some detail for a few broods in one season only (de Leeuw & Beekman 1991). In the rather uniform habitats of the Groningen study area that growth curve may be fairly typical for all pairs. But elsewhere, with more variable habitats between territories, the shape of the growth curve could vary widely with habitat and season. The most appropriate timing of incubation for a particular habitat might become more predictable with a female's experience of a particular site: Walter, *et al.* (1991) found a significant effect of (female) experience in improving breeding success around Oxford, UK.

Conversely, seasonal effects will reduce a swan's ability to learn rapidly from experience, and will favour 'robust' strategies that work well in many circumstances (assuming that the circumstances for cygnet growth cannot be accurately predicted at the time of laying).

The present model assumes that all eggs are laid at two day intervals, which is not always the case (though we do not understand the reasons for the variation). Reducing the laying interval both reduces the risk of clutch loss and could slightly alter the expected survival of cygnets raised following earlier incubation.

The present model also assumes that all eggs have constant volume. However, egg volumes vary appreciably. Beekman (unpublished) gives a range of 300 to 350 cc: Bacon & Mountford (1990) give a range of clutch means (per female) of 315 to 350. In contrast to several types of birds larger eggs in swans also seem to reflect better quality eggs (Birkhead 1984). The volumes of eggs are also significantly more consistent within than between females (or sites) and are correlated to esterase genotype (Bacon & Mountford 1991). Hence it is possible that late-breeding females, or those in poor quality habitat for cygnet growth, might increase their eggs' volumes and qualities to promote higher survival of fewer cygnets. Conversely, females in good quality habitat for cygnet growth might decrease their eggs' volumes and qualities to permit an extra egg. However, the data on observed egg volumes suggest that only females able to lay 6 to 9 'large' eggs would have sufficient total egg mass to lay one extra egg at the 'small' end of the observed range of egg volumes (the calculation is quite sensitive to the assumed lower limit of viable small eggs, 300 to 315 cc).

Further options and constraints for the female

In the present model the physiological constraints assume all females start incubation at a weight of 9.0 kg: while this is a good approximation, Beekman's data show it is not strictly true; deviations occur in both directions. Presumeably the heavier females stress themselves less and would be better able to lay replacement clutches rapidly; the lighter females will get rather close to the 'lethal limit' by the end of incubation. These deviations might represent low and high risk strategies: the relative benefits would probably depend on food availability, first to the laying female and then to the growing cygnets, about which we know too little to speculate usefully.

The present model does not envisage that females would have problems with regaining sufficient weight to complete primary moult satisfactorily: this may not always be true.

Options for the males.

It would at first sight seem that males could ease constraints on the female considerably by assisting with incubation. We would be intrigued to know why they do not (see Beekman 1991 for some discussion of this).

Developments of the model

The existing model works for 'average' swans in 'average' conditions. Given data on cygnet growth in different habitats/territories it should be possible to refine predictions of over-winter survival, based on hatching dates, growth rates and winter severity. Similarly winter severity data should permit us to say something about the timing and success of breeding the following spring. In the first instance we would expect winter temperature to affect female condition in late winter, (day-60 weights in model), producing the same general effects demonstrated by Walter *et al.* (1991) for the Oxford study and Beekman (1991) for the Groningen area. At a more detailed level we might expect that the position and shape of the nutrition constraint curve would vary with spring weather as well as with habitat.

More speculatively we might try and extend the concepts to cover development to maturity. Several workers (Bacon & Coleman 1986, Andersen-Harild 1981, van Dijk & van Eerden 1991) have shown that non-breeders may be stressed during moult, an effect that may be more pronounced in males. Since males need to grow more it could be that nutritional demands sometimes limit their development and might even delay their ages of first maturity.

The existing model, with suitably altered offspring pay-offs and nutrition constraints could be used for arctic breeding swans. Here, however, a useful extension to consider would be the consequences of the extra energetic constraints of migration. As soon as the basic energetic requirements are sufficiently well known it should be possible to attempt this and check if existing beliefs about routes and stop-over sites are consistent and adequate.

Invalidating the model

We undertook the physiological model mainly as an exercise in data collation, and were surprised, and pleased, by the interesting biological questions it has raised. However, before its implications are taken too seriously, greater efforts to invalidate it should be made than we have been able to achieve with Beekman's existing data. If, by the time of the 4th Swan Symposium, it has been firmly and irrefutably invalidated it will have served a useful purpose! Should anyone wish to attempt this, we would direct their attention to the following points.

We believe the start of incubation to be a more useful reference date than the date of laying of the first egg. As the incubation period is very constant, incubation dates (and the subsequent hatching dates that the females may be optimising) vary less than dates of laying the first egg (which are affected by both clutch size and egg laying interval). But female weight, clutch dates and size probably all need to be analysed together.

The model's predictions are highly sensitive to knowing the weights/conditions of females in late winter, at a time when females are hard to catch. Female's conditions are better estimated by correction for body size, so suitable biometric data are necessary (but obtainable at other times of year). It would help if different workers used the same measurements.

The outcome of the model, especially the location and extent of the 'flat shoulder' of the response surface, depends on the interaction of the offspring pay-off curve and the nutrition constraint curve. Both need to be known with much more precision. Experimental manipulation is probably required to adequately assess the shapes of the extremes of the offspring pay-off curve. Both curves need estimating for the same study site/habitat.

Further details of cygnet growth curves, in different habitats and years, might allow better prediction of first winter survival between broods within study areas.

Food quality at moulting sites may limit rates of development to maturity and, especially where winter conditions are severe, breeding prospects the following spring.

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