



Two explanations of the dawn chorus compared: how monotonically changing light levels favour a short break from singing

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I used optimality modelling to compare two of the most plausible and general explanations for the dawn and dusk peaks in bird song output. Kacelnik's explanation is that foraging is inefficient in poor light, but that social interactions are less affected, making singing more worthwhile than foraging. McNamara et al.'s explanation is based on stochasticity in foraging success and overnight energy requirements; it has been extensively analysed with stochastic dynamic programming models. Both explanations are now incorporated into this sort of model. I used various functions to link success of foraging and singing to time of day, but assumed that above some light level there is no further effect. Kacelnik's explanation has as strong an effect as stochasticity in generating dawn and dusk choruses. It also predicts short pauses in the singing output just after the dawn chorus and before the dusk chorus. The former arises because birds delay foraging when it will become more profitable later, until foraging success reaches a plateau, when the energetic debt accumulated makes them forage. The principle of this see-saw double switch in behaviours may apply to other explanations for the dawn chorus, and to other shifts in behaviour when conditions change gradually. The model predicts that from day to day cloud cover determines when a dawn chorus starts, but that overnight temperature and wind strength have more effect on chorus intensity and duration. I discuss what sort of observational and experimental data on singing routines would better test this model.

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In many situations the net benefit from a behaviour changes gradually and predictably over time, with the consequence that animals shift from one behaviour to another. One might expect a monotonic change in benefit to result in a unidirectional shift in the frequencies of each behaviour. However, suppose that you must write both research papers and grant proposals, and that you learn that grants will be getting harder to win over the next year; after that they will remain hard to win. You should put extra time into submitting grant proposals this year at the expense of papers. But then next year you will have to compensate by putting more effort into papers than into proposals (because you have a deficit of recent papers, or maybe you will anyway have depleted your store of good ideas for proposals). In the following year, you may again aim for a more balanced output of papers and proposals, even though winning grants remains as hard. This see-saw double switch in behaviour arises because of the state-dependent nature of the

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decision: allocation of effort depends on your 'credits' in papers and proposals.

I propose that the see-saw double switch is likely to be a widespread phenomenon in biology. Another example might be a bush that must allocate resources to root growth or leaf growth. Suppose that leaves become more valuable later in spring when there is more light and less chance of a frost. So, by analogy with the earlier example, we might predict root growth initially predominating over leaf growth, then the reverse to restore the balance in leaves and roots once the weather is suitable for leaves, then a more matched output of new leaves and roots to maintain this balance. One could idly think up many such potential examples, but the rest of this paper models in detail a single example that has already attracted empirical and theoretical interest. It involves the effect of increasing light levels at dawn on how birds pattern the timing of their singing and foraging.

A peak in the singing activity of birds at dawn is a widespread, although not universal, phenomenon (Staicer et al. 1996). Many ultimate explanations for this dawn chorus have been proposed (Mace 1987; Staicer

et al. 1996), and several have been supported by empirical tests of their predictions or assumptions (e.g. Kacelnik 1979; Mace 1989a; Slagsvold et al. 1994; Thomas 1999a, b). Because these explanations are mostly not conflicting, more than one could play a role, even in the same species. One might imagine that the processes would combine to accentuate the dawn chorus. In this paper I incorporate two different explanations into a formal model that had involved only one of them. One of these explanations, based on the change in foraging success with light levels, makes a novel and unexpected prediction for the shape of the singing routine at dawn: two peaks, separated by a pause when it gets light enough for birds to feed fully efficiently. This is a manifestation of the see-saw double switch described above. Few good data exist to test this prediction, but I present some favourable evidence below. Modelling suggests which explanation has more effect on the shape of the daily singing routine, and which has more effect on the day-to-day variation in the intensity and timing of the dawn chorus.

EXPLANATION 1: STOCHASTICITY OF OVERNIGHT ENERGY REQUIREMENTS

One ultimate explanation for the dawn chorus comes from computer modelling the optimal level of energy reserves in a stochastic environment (McNamara et al. 1987; Houston & McNamara 1987; Hutchinson et al. 1993; Hutchinson & McNamara 2000). The first step in the argument is that most diurnal species of birds must store enough energy reserves by dusk to survive overnight, when they cannot feed. Overnight energy requirements are partly unpredictable, owing to variation in the weather, and birds should try to store reserves adequate for almost the worst case. Consequently, after most nights they have a surplus. High reserves are unnecessary at dawn because birds have all day to build up reserves for the next night. Furthermore, carrying excess reserves has a cost, through both increased energetic expenditure when flying and increased vulnerability to predation (Witter & Cuthill 1993). Therefore, if birds are going to sing sometime, dawn is a good choice because feeding has less benefit then.

It will help to have formalized this argument by considering the optimal 'policy', calculated using stochastic dynamic programming (Mangel & Clark 1988; Houston & McNamara 1999). The policy specifies what action to perform at each time given an individual's 'state'. Here the single state variable is energy reserves. The form of the optimal policy is that the bird should sing if above a particular switchpoint level of reserves, and forage if below. This switchpoint is low and constant throughout the morning, but rises through the afternoon towards the levels necessary for dusk (Fig. 1a). After most nights reserves are well above the morning switchpoint, so birds sing their dawn chorus and reserves consequently fall. When reserves fall below the switchpoint, feeding takes them above it again, so singing alternates with feeding through the morning, leading to a consistent average level of singing (referred to here as the 'morning

plateau'). As the switchpoint level rises in the afternoon, feeding predominates over singing. A quiet afternoon is indeed a feature typical of many real singing routines, as is a dusk chorus. The dusk chorus arises in the model because of the stochasticity in foraging success: birds dare not leave raising their reserves to the last minute in case of a late run of bad luck. Usually they reach the intended level of reserves early, and then they can afford to sing.

Hutchinson et al. (1993) performed an extensive sensitivity analysis to establish how robust this pattern was to variation in the parameter values. As expected, the initial dawn chorus disappears if there is little stochasticity in overnight energy requirements (Fig. 1b). If we assume that costs of being overweight are usually greater when actively foraging than when singing, dawn levels of song are below the level of the morning plateau unless there is sufficient stochasticity in overnight energy requirements. The intensity of the dawn chorus, as well as the intensity and duration of the morning plateau, are reduced by a lower availability of energy (i.e. less food relative to energy expenditure) and by a greater stochasticity in foraging success. In the extreme, this can lead to no dawn chorus or morning plateau, but a consistent rise in singing levels from dawn to dusk. The model has been expanded to incorporate time-of-day variation in the benefits from singing (McNamara et al. 1987; Hutchinson et al. 1993), some ability to predict the forthcoming night's weather (Hutchinson & McNamara 2000), an additional benefit for sustained, rather than intermittent, singing (Hutchinson et al. 1993), and benefits of synchronizing with rival singers (Houston & McNamara 1987). These elaborations can each favour somewhat different routines, but the latter two tend to intensify and prolong the dawn chorus.

Perhaps the most convincing tests of the hypothesis have shown a generally consistent positive relationship between overnight temperature and song output at the succeeding dawn (reviewed in Thomas 1999a; see also Godfrey & Bryant 2000). Thomas & Cuthill (2002) found a positive relationship between dawn mass and dawn song output. Tests based on manipulations of food availability are also broadly supportive of the underlying assumptions (Thomas 1999a, b, and references therein), but Hutchinson & McNamara (2000) discussed some problems in interpreting such manipulations. Staicer et al. (1996) pointed out that the hypothesis incorrectly predicts greater dawn choruses earlier in the breeding season when nightly energy requirements are more variable, but many other factors are confounded with season, so this argument does not seem conclusive.

EXPLANATION 2: INEFFICIENT FORAGING

Kacelnik (1979) proposed that birds sing more at dawn and dusk because the low light levels make feeding relatively unprofitable. Furthermore, colder temperatures at these times will make arthropod prey less active, and thus doubly hard to find (Avery & Krebs 1984).

A related argument is that, in some species, females may become active only when foraging is profitable, and

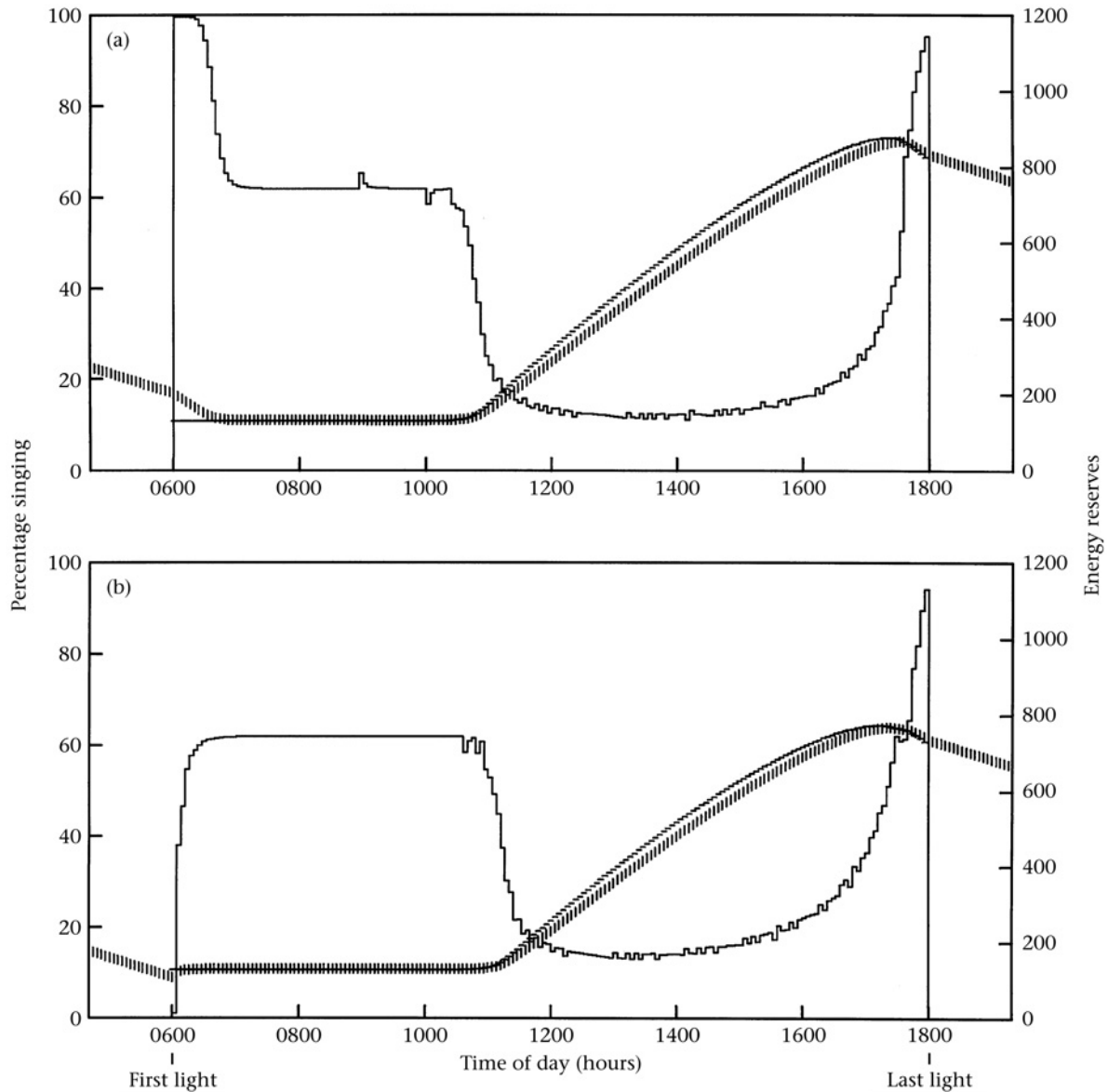


Figure 1. Optimal singing routines with sudden transitions between night and day and with (a) stochasticity in overnight energy requirements, as in Explanation 1 (see text), or (b) no such stochasticity. In this and succeeding figures: continuous line=% of unpaired singing members of the population; horizontal dash=switchpoint level of reserves above which singing is best; vertical bar=mean level of reserves in unpaired members of population. Parameter values are given in the [Appendix](#), except that in (b) total energy requirements overnight always= $R_{\text{normal}} \times 180$.

that a male stops singing when his mate emerges from her roost (Mace 1986; Slagsvold et al. 1994). Empirical evidence in several species supports this dependence of the male singing routine on female emergence times (Otter & Ratcliffe 1993; Slagsvold 1996; Welling et al. 1997). However, this explanation for the dawn chorus cannot apply to unpaired birds, and I do not consider it further here.

In isolation, Kacelnik's argument is incomplete, because it does not explain why the singer wakes up before it can feed, or why it does not wake up much earlier so that the dawn chorus is spread over a longer period. In a model that allowed singing to have an equal

benefit at all times of day and night but feeding to be possible only during the day, the optimal routine was to sing mostly after dusk (Figure 10 in Hutchinson et al. 1993); this routine is reminiscent of nightingales, *Luscinia megarhynchos* (Thomas 1997), but quite different from most birds. So it is necessary to make the assumption that the audience is unresponsive overnight until only shortly before foraging becomes possible. This seems reasonable: birds could listen to mates or neighbours singing overnight, but much social behaviour contingent on that signal (e.g. a sneaky copulation, or chasing an intruder) might plausibly occur only when there is some light, so the best policy may be for birds to ignore song until

shortly before dawn. I expect such social interactions to be performed fully effectively at low light levels at which foraging is still inefficient.

Accordingly, and for consistency, the model that I develop below assumes not only that the efficiency of foraging increases gradually at dawn, but that also the increase in the effectiveness of singing is gradual, although the maximum is reached earlier for singing than for foraging.

METHODS

To establish the relative importance of these two explanations, I incorporate the effects of low light levels into the type of stochastic dynamic programming model already used to analyse Explanation 1. So I am using an optimality approach to predict singing routines that should evolve if light levels affect foraging efficiency. The design of the model follows that in [Hutchinson et al. \(1993\)](#). The Appendix gives a more technical explanation of the model than provided here and also baseline values of the parameters.

In the model, time is divided into intervals of 4 min. A bird spends all of each interval either singing, foraging or resting, and which is best (which it chooses) depends only on the time of day and on its energy reserves. Foraging and singing are not possible during the night, and in the original model the transition between night and day was sharp, an assumption modified below. A bird forages because food will increase its reserves, but it may be unsuccessful: then reserves will fall through metabolic expenditure. Each activity entails a different metabolic expenditure, and expenditure when foraging and singing increases with existing reserves (because heavier birds require more energy to fly; their extra risk of predation is not incorporated here but would tend to have a similar effect in limiting how much reserves are accumulated). All changes in reserves are stochastic, and there is an extra component to stochasticity in overnight energy requirements: in a proportion of nights energy expenditure of resting is higher than usual because of bad weather.

If reserves fall to 0, a bird is declared dead from starvation, so birds with low reserves should forage. At high energy reserves it pays to sing, because a singing bird has a probability p_{pair} of attracting a mate. This is not necessarily realistic but is a convenient way to introduce a reward for singing into the model. A paired bird does not sing further, and, if it does not starve, it is awarded a score twice that of merely surviving unpaired. I calculate the policy that maximizes the expected value of this score at the end of a time window that is stochastic in length and finishes on average 10 days ahead. Dynamic programming is the numerical algorithm used for this calculation. The resulting optimal policy is a rule of what behaviour to choose when in each reserve level at each time of day, and typically it is as simple as singing if above a critical switchpoint level of reserves and foraging if below, with the switchpoint increasing through the day.

I then start with a population of birds with an arbitrary level of reserves, and let them follow the rules of the policy over many days. Because of stochasticity, reserve levels differ over the population, but the distribution among the unpaired surviving birds converges to be the same at any given time of day. In the figures, the average value of this distribution is shown as a vertical bar; the stepped curve shows the proportion of unpaired birds in the population that sing, as a result of having reserves higher than the current switchpoint specified by the policy (horizontal dash).

In this paper I modify this model to incorporate gradual changes in light intensities at dawn and dusk. Were Earth to lack an atmosphere or moon, and the sun to be a point source of light, light intensity on a horizontal surface would change following a sine curve with a 24-h period, but with the bottom of the curve missing because the sun is hidden at night ([Kirk 1983](#), page 33). At the equator at an equinox exactly half the sine curve is present, so that the increase in light at dawn is initially roughly linear. During the summer in temperate regions, more of the sine curve is present, so that this increase is more sigmoid. The atmosphere makes light intensities change more gradually at dawn and dusk, so that even in winter the relation is somewhat sigmoid. How these changing light levels translate into foraging success is more uncertain, and will vary between species and habitats. I assume that increasing brightness has a diminishing effect on foraging success, eventually giving no further benefit, and I ignore any continuing effect of increasing temperature on prey detectability or catchability. Indeed, [Kacelnik \(1979\)](#) found in the laboratory that the foraging success of great tits, *Parus major*, had more or less reached a plateau at light levels corresponding to 30–60 min after their usual start of activity.

In the original model, if a bird foraged during a time interval, it found a fixed quantity of food with a constant probability p_{food} , and no food otherwise. In the new version, p_{food} depends on time of day. Time of day does not affect the quantity of food gained in those time intervals when food is found; such an effect might be more realistic, but is more awkward to implement, and both ways of altering the average food gain are expected to have similar consequences. At night, $p_{\text{food}}=0$, but from first light until time T_{food} after first light, p_{food} increases; then p_{food} remains constant until T_{food} before last light. [Figure 2](#) shows various plausible functions relating p_{food} to time of day between first light ($t=0$) and T_{food} . The decline in p_{food} at dusk is kept symmetrical with its increase at dawn.

In the original model, if the bird sang in a time interval, it had a constant probability p_{pair} of pairing with a mate. Now p_{pair} shows the same relation with time of day as does p_{food} , except that the function reaches a plateau at time of day T_{pair} , where normally $T_{\text{pair}} < T_{\text{food}}$ (i.e. social interactions require less light than foraging). I usually take $T_{\text{pair}}=40$ min, but the results are robust to using other similar values. In the original model birds rested only at night, but now that p_{pair} is low around dawn and dusk, they may choose to rest also at these times during the day.

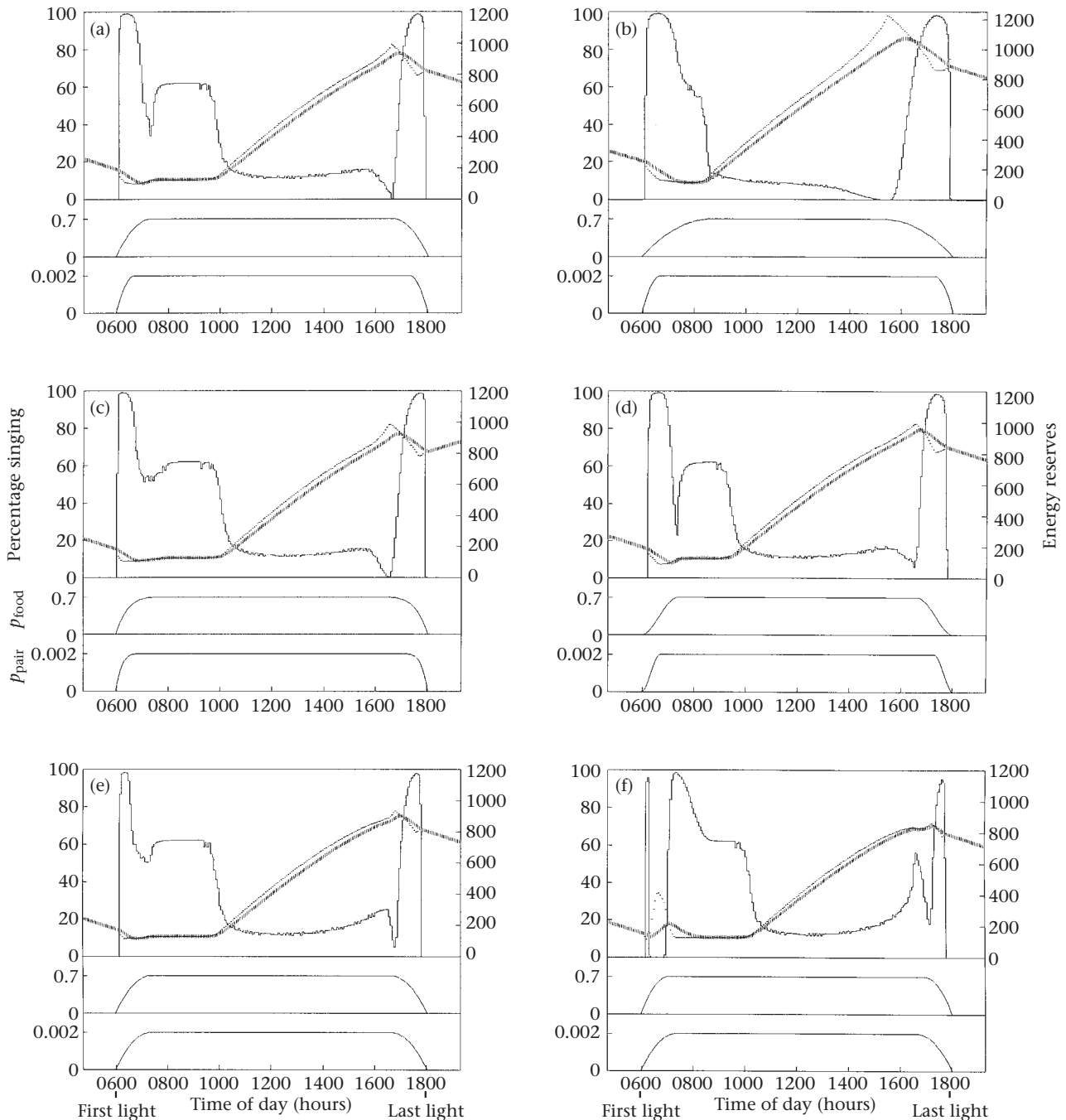


Figure 2. Optimal singing routines with gradual transitions in pairing and foraging success through twilight, as in Explanation 2, and no overnight stochasticity. Parameters follow those in Fig. 1b, except that p_{food} and p_{pair} (the probabilities of finding food and pairing) are functions of time for a period of T_{food} and T_{pair} , respectively, after 0600 and before 1800 hours. In each case, the relation with time is symmetrical about midday, and p_{food} and p_{pair} follow the same function with different parameter values. In (a)–(c), (e) and (f), for the period after first light $p_{\text{food}}(t) = 0.7(1 - ((T_{\text{food}} - t)/T_{\text{food}})^N)$, which has a maximum T_{food} after 0600 hours. (a) $T_{\text{food}} = 80$ min, $T_{\text{pair}} = 40$ min, $N = 2$. (b) $T_{\text{food}} = 160$ min, $T_{\text{pair}} = 40$ min, $N = 2$. (c) $T_{\text{food}} = 160$ min, $T_{\text{pair}} = 80$ min, $N = 6$. (e) $T_{\text{food}} = 80$ min, $T_{\text{pair}} = 80$ min, $N = 2$. (f) $T_{\text{food}} = 60$ min, $T_{\text{pair}} = 80$ min, $N = 2$. In (d), p_{food} and p_{pair} over these intervals instead follow the cubic function that forms a spline with the constant-valued functions either side; $T_{\text{food}} = 80$ min, $T_{\text{pair}} = 40$ min.

RESULTS

Dawn and Dusk Choruses

Figure 2 presents the consequences of gradual changes in feeding and pairing success at dawn and dusk. Here

overnight energy requirements are nonstochastic, so as to eliminate Explanation 1 for the dawn chorus; comparison with Fig. 1b (nights also nonstochastic, but step-function changes in p_{pair} and p_{food}) isolates the effects of the gradual changes. A side-effect of the gradual changes in

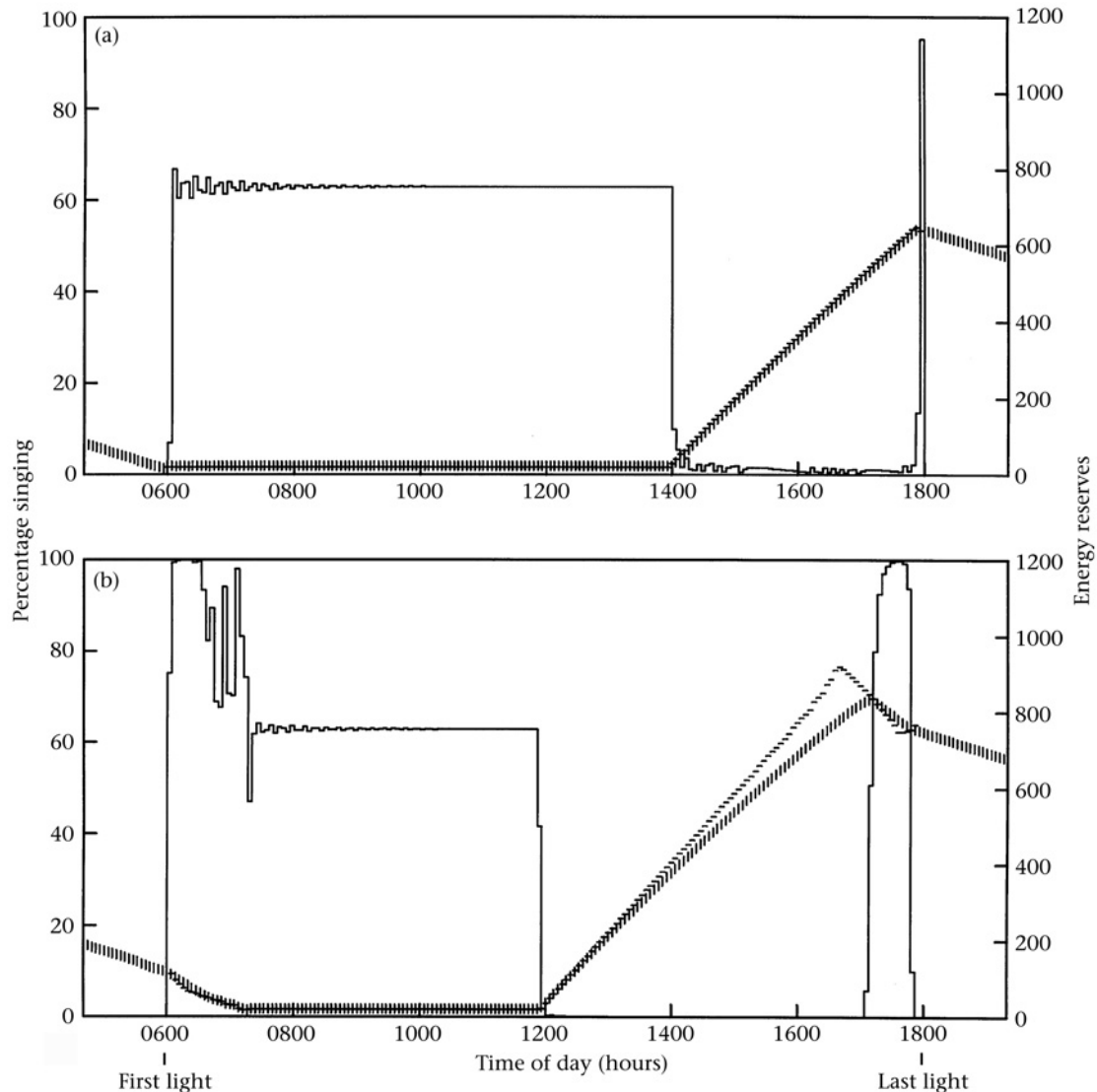


Figure 3. Gradual changes in light levels cause a dusk chorus. Foraging and pairing successes change as a step function in (a), but gradually (as in Fig. 2a) in (b). Parameters as in Fig. 1b, except that daytime stochasticity is reduced to almost eliminate the generation of a dusk chorus by Explanation 1: $e=22.4$, $p_{\text{food}}=1$, $\eta_s=1.5$, $\eta_f=1.5$.

p_{food} at dawn and dusk is that the total availability of food over the day is less than when p_{food} changes suddenly. This reduction decreases the level and duration of the morning plateau of song output. Such differences in the routines in Fig. 2 are not of interest here, because they can be removed by altering other parameters affecting food availability.

Gradual changes in foraging success indeed produce a strong dawn chorus (Fig. 2), and this can last longer than that produced by overnight stochasticity in energy requirements (Fig. 1a).

The dusk chorus is consistently longer than when foraging success drops suddenly at dusk. However, part of the reason for the dusk chorus in Fig. 2 might be the same as for that in Fig. 1, that is the stochasticity in foraging success and energy expenditure. In Fig. 3 I

reduced this stochasticity until the dusk chorus is much shortened in the case when foraging success follows a step function (Fig. 3a). (This stochasticity cannot be eliminated completely for reasons to do with how the optimization technique interpolates between grid points, and I retain more than the minimum stochasticity here so that the singing routine does not contain many artefactual jumps.) Reintroducing a gradual transition in foraging success reintroduces a fuller dusk chorus (Fig. 3b). So Kacelnik's argument in isolation does explain the dusk chorus.

Kacelnik's argument does not explain why real birds start to sing at dawn at light levels well below those at which the dusk chorus ends. And it predicts dawn and dusk choruses of similar intensity, whereas the usual pattern is for the dawn chorus to be stronger.

Sensitivity Analysis

By altering each parameter one at a time, I examined whether the dawn and dusk choruses are robust outcomes when foraging success changes gradually at dawn and dusk. They are more robust and more equal in intensity than with Explanation 1. Altering parameters to reduce energy intake or increase energy expenditure shortens the morning plateau; singing may then occur only at dawn and dusk, and further reductions in energy availability make both these peaks disappear at the same rate. Unlike with Explanation 1, one cannot generate a routine with steadily increasing song output from dawn to dusk either by decreasing food availability or increasing its stochasticity (cf. Figures 4 and 5 in Hutchinson et al. 1993). Increasing the cost of singing has different effects from altering other parameters that affect energy availability: the length of the morning plateau changes little, but its intensity is reduced; the dawn and dusk choruses are shortened and may be less intense. Making the mass-dependent costs of singing higher than those of foraging (as in species with aerial displays) shifts singing effort from dusk to dawn, although the symmetry remains higher than with Explanation 1 (cf. Figure 3 in Hutchinson et al. 1993).

The effects of altering how foraging and pairing success change with time of day are dealt with below and in Fig. 2.

Pauses in the Song Output

It is characteristic of the singing routines in Fig. 2 that the dawn chorus is followed by a lull, after which song output rises again to the level of the morning plateau (the see-saw double switch). The reason is this. Soon after first light singing becomes as rewarding as it will ever get, but foraging success continues to increase; consequently, birds should put off foraging until later (to sing, then forage is better than to forage, then sing). When foraging success has reached its plateau, or nearly so, further delay is no advantage, and by then birds are low in reserves. Replenishing reserves causes the pause in singing. Once foraging has replenished reserves, birds again sing, but now more frequently alternate singing with foraging.

This explanation can also be expressed in terms of the policy (horizontal dashes in Fig. 2). There is a switchpoint level of reserves above which singing is the best option. The fall in the switchpoint immediately after first light is caused by singing becoming more rewarding relative to resting. The result of the fall is that reserves are above the switchpoint and remain so even when birds consequently sing, thus generating the dawn chorus. As foraging becomes more successful, resting is no longer ever optimal, and the switchpoint level of reserves above which singing is better than foraging rises (i.e. it pays to forage at reserve levels at which before it was best to sing). The switchpoint rises more steeply than the mean level of reserves, so most birds whose reserves fall below the switchpoint remain below the switchpoint (i.e. remain silent) until the switchpoint stops rising so steeply, which occurs when foraging success increases more slowly. If the

increase in foraging success is steeper over this critical period, the switchpoint rises faster, and thus more birds remain below the switchpoint, which accentuates the pause (Fig. 2d; cf. Fig. 2c where the increase in foraging success is less steep at this time).

That a gradual increase in foraging success causes a pause in singing was unexpected, but the verbal explanation suggests that it should be a general phenomenon. It indeed persists if we alter the function by which foraging success changes, or the duration of the change (Fig. 2). However, if food is scarce relative to energetic demands, the switchpoint continues to rise towards the necessary levels at dusk, eliminating the morning plateau and thus obscuring the pause (Fig. 2b).

Even if foraging success increases at the same rate and time as pairing success, there are still dawn and dusk choruses, although shorter, and the pauses may still occur (Fig. 2e). This is because, although both probabilities of success change in concert, the fitness advantage from singing rises more steeply with time than that from foraging. If foraging success reaches its maximum before pairing success (less plausible, but perhaps birds seek to inspect details of plumage before pairing), there may still be a burst of song shortly after first light, but then there is silence while birds feed (Fig. 2f). This raises reserves enough to generate a pronounced peak in song when pairing success later approaches its maximum value. Although I have concerns about the model's assumptions, this pattern matches some observed routines (see Discussion for examples).

Other sorts of gradual improvement in foraging may also cause a pause. For instance, even if foraging success is constant after first light, predation risk when foraging might decrease as the light improves. Again the model predicts a dawn chorus and a pause in singing (Fig. 4a), as long as predation risk changes sufficiently to make birds put off foraging until later. Another way in which the relative benefits of singing and foraging can change is if the profitability of foraging stays constant, but singing becomes less rewarding later in the morning. This fits several other hypotheses used to explain the dawn chorus: that early in the morning females are more fertile, that newly arrived females and vacated territories accumulate overnight, and that sound transmission is better at dawn (Mace 1987 and references therein; but see Birkhead et al. 1996; Dabelsteen & Mathevon 2002; Thomas et al., in press). In Fig. 4b, I assume that the chance of a reward from singing (p_{pair}) rises to a maximum shortly after dawn, then gradually declines to half of the maximum value, and then remains constant until dusk. Foraging success is kept constant throughout the day, which is not realistic, but serves to isolate the effect of the changing reward from singing. Again the model predicts a pause separating the dawn chorus and the morning plateau.

A second pause in singing activity, just before the dusk chorus, is a consistent feature of models in which foraging success declines gradually at dusk (Figs 2, 3b). The reason is that if birds know that foraging success will shortly decline, they should forage intensively while success remains high.

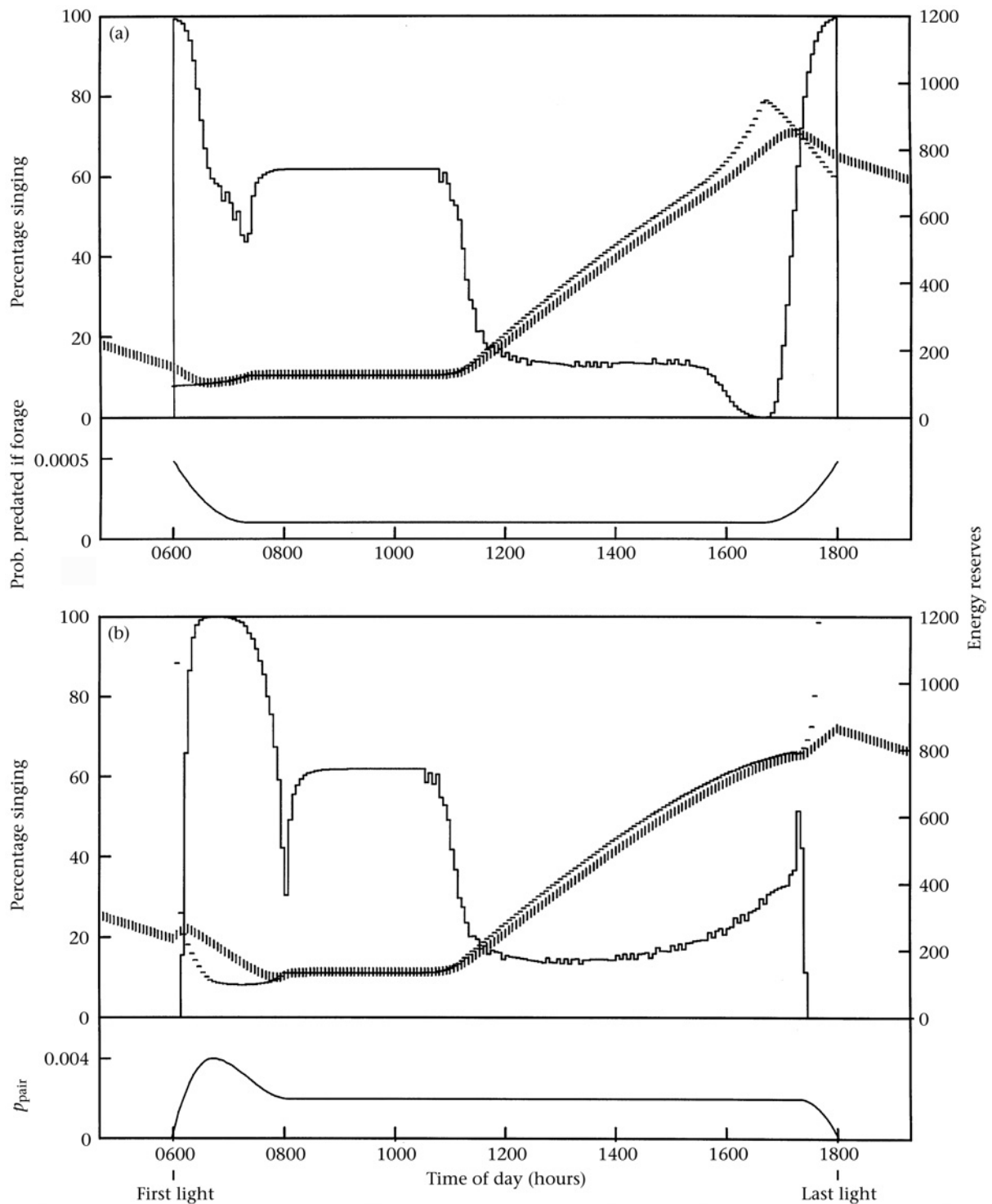


Figure 4. Alternative ways to generate a pause by gradually altering the relative advantages of singing and foraging through the twilight periods. (a) If an animal forages, it is more likely to be predated in the twilight than in the middle of the day. Here foraging success and pairing success change suddenly at 0600 and 1800 hours, remaining constant during the day. (b) Pairing success increases gradually at dawn but then decreases again, then remaining constant until dusk. Here foraging success is a step function and there is no predation. Other parameters as in Fig. 1b.

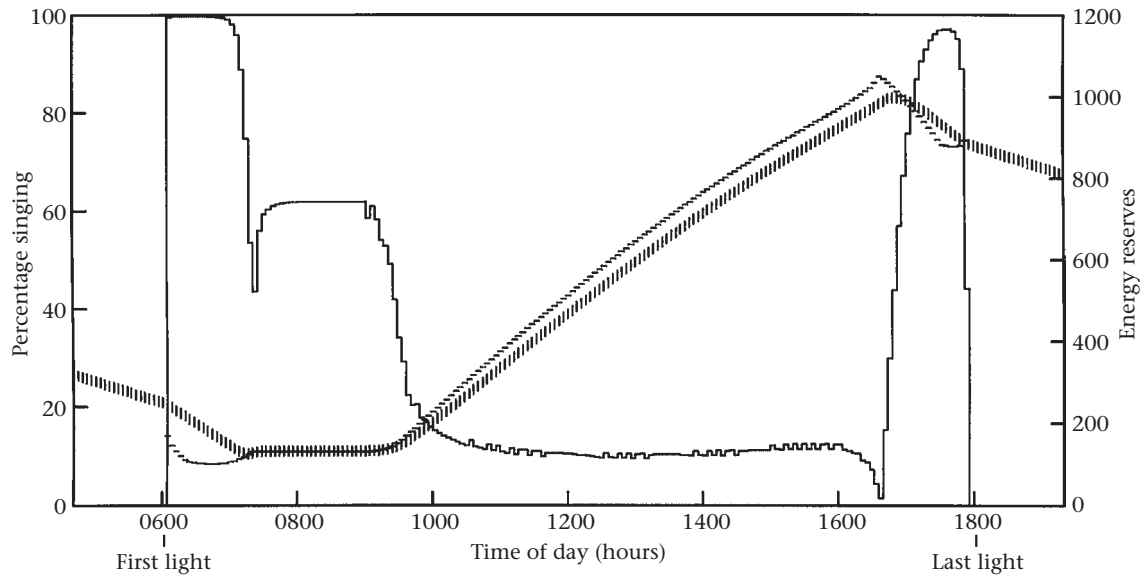


Figure 5. Explanations 1 and 2 integrated. Overnight stochasticity and other parameters as in Fig. 1a, combined with the gradual changes in pairing and foraging success shown in the lower parts of Fig. 2a.

Which Explanation is More Important?

In the real world these exist both stochasticity in overnight energy requirements and gradual changes in foraging efficiency through twilight. In the model either factor can generate a dawn chorus. Can we use the model to judge which explanation is more important? One sense in which to answer this is to consider the shape of the optimal routine on an average day. In Fig. 5 there is both stochasticity in overnight energy requirements (quite high levels) and a gradual change in foraging success through twilight. The optimal routine then looks more like that resulting from the gradual change and no overnight stochasticity (Fig. 2a) than like that resulting from overnight stochasticity and a step change in foraging success (Fig. 1a). There is a pause after the dawn chorus, and adding overnight stochasticity seems merely to have intensified the dawn chorus a little. Thus, although overnight stochasticity in energy requirements may be higher in spring than in summer, or at some localities, we do not predict this to affect the routine much. The sun rises more quickly near the equator and near an equinox, and we do predict this to shorten the dawn chorus. (At an equinox, twilight lasts 1.3 times as long in Rome as at the equator, and 1.5 times as long in Stockholm as in Rome; in London, twilight is 1.3 times as long at a solstice as at an equinox.) Comparison of three great tit populations from different latitudes showed a nonsignificant trend in the predicted direction (Mace 1989b). However, such comparisons between seasons and latitudes are confounded with changes in, for example, food availability, the benefits from singing, and the duration of the day, so I would be circumspect about such evidence.

Another sense in which to answer which explanation is more important is to consider day-to-day variation in the routine. On some days the night will have been colder or

windier, using up more energy reserves, and on some days cloud cover will delay when it starts to get light and for how long foraging success increases. I now investigate which source of variation has more effect on the population-average singing routine each day.

Small isolated clouds can increase light levels reaching open ground by 5–10%, and such an effect seems likely to be particularly strong when the sun is below the horizon (Kirk 1983, pp. 30, 35); in forest the increase is typically about 15% (Endler 1993). In contrast, heavy cloud can reduce light levels by 90%, and I will assume that this negative effect is the main source of variation. Measurements of light levels near Bristol and Cardiff in May, over about 90 min at the time of the dawn chorus, showed a roughly linear relationship between log(light intensity) and time (R. J. Thomas, personal communication). The slopes of these graphs mean that a 90% reduction in light intensity caused by heavy cloud would merely shift each graph 14–18 min later, which was the sort of variation observed. Accordingly, in Fig. 6 the policy is adapted to cope with such day-to-day variation in the effective length of the night caused by varying cloud cover at dawn. Cloud cover remains the same within a morning but changes unpredictably overnight; for simplicity, there is no variation in cloud cover at dusk. The solid and dashed lines in Fig. 6 show the population routines on, respectively, a clear morning and a very cloudy morning (20-min delay). The shapes are similar, although when dawn is later, the dawn chorus starts later, and it lasts slightly shorter (though nevertheless later) because the longer night has depleted further reserves. Empirical research also shows a strong effect of day-to-day variation of light levels on the start time of the dawn chorus (e.g. Leopold & Eynon 1961).

In Fig. 6 the optimal policy is geared to cope also with variation in overnight energy requirements. There

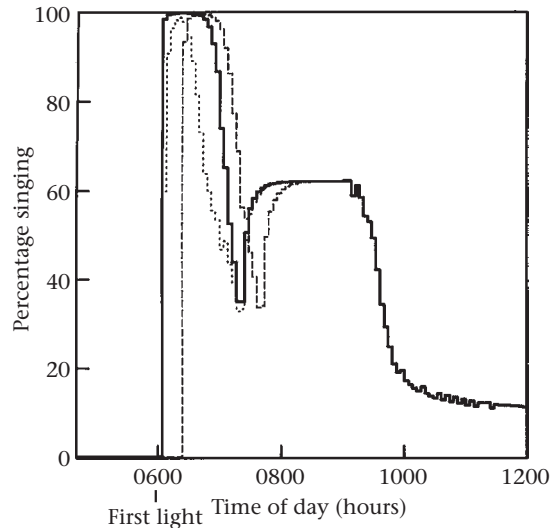


Figure 6. How day-to-day variation in weather affects the optimal routine in a model incorporating both Explanations 1 and 2. Only the first half of the day is shown. The policy is adapted to a 10% chance of a 10% higher overnight energy expenditure ($R_{\text{cold}}=3.85$) and to equal probabilities of cloud delaying dawn by 0, 8 or 20 min (but the shapes of the functions linking foraging and pairing success to time are unchanging, and as in Fig. 2a). Other parameters as in the Appendix. Thick solid line is routine after a night of normal temperature with no cloud. Dashed line is after a night of normal temperature with dawn 20 min late. Dotted line is after a cold night with no cloud.

is a 10% chance of a night requiring 10% more energy than normal, which is modest variability, at least in a temperate spring. Dark-eyed juncos, *Junco hyemalis*, require ca. 10% more energy if overnight temperature falls from 10 to 0°C, or if wind speed increases from 0.6 to 2 m/s (Bakken et al. 1991), and the effect of temperature on mass loss appears greater in other species (Lehikoinen 1987). In the model, a cold night causes a considerable reduction in the duration of the dawn chorus (dotted line in Fig. 6). And if I increase variability so that there is a 5% chance of a 20% increase in mass loss, after cold nights the dawn chorus is less intense even than the morning plateau. This sensitivity to overnight weather conditions agrees with empirical results (Thomas 1999a). However, we expect a smaller effect if birds can predict the day before how cold the night will be (Hutchinson & McNamara 2000; Thomas & Cuthill 2002).

My conclusion is that Explanation 2 is more important in determining the shape of the routine on average days, and also affects day-to-day variation in the start time of the dawn chorus, and maybe in its duration. However, stochasticity in overnight energy requirements has the greater effect on day-to-day variation in the intensity and duration of the dawn chorus. In practice light levels at dawn and overnight energy usage do not vary independently. Cloudy nights tend to be warmer, but are also effectively longer. However, a 20-min lengthening has little effect on total overnight energy use compared with typical variation in temperature and wind speed.

DISCUSSION

To summarize the results, modelling either explanation in isolation generates dawn and dusk choruses fairly robustly, but a pause in these choruses appears when we make light levels gradually change foraging success. In nature we should expect both this gradual change and stochasticity in energetic expenditure and gain; a model integrating both explanations also produces choruses with pauses. This model predicts variation in temperature and wind to have most effect on the intensity and duration of the dawn chorus, but variation in cloud cover to affect more strongly when it starts.

McNamara et al. (1987) already had the idea of incorporating Kacelnik's (1979) explanation for the dawn and dusk choruses into their stochastic dynamic programming model. They too reported a strong effect on the dusk chorus, as long as costs of being overweight were not too high, but the effect on the dawn chorus was more minor and they did not observe a pause following it. The differences with my results arise because: (1) in their model foraging success increased linearly until noon, and then decreased linearly until dusk, rather than reaching a plateau; (2) foraging success changed by only 2.5% over the day, at least in the routines illustrated. I consider my modelling of the changes in foraging success more realistic.

Kacelnik's verbal explanation for the dawn and dusk chorus is so plausible that its strong effect when incorporated into the model is not surprising. Less certain was how this explanation would interact with the other explanation for the dawn and dusk choruses based on stochasticity in energy expenditure and gain. However, the most startling consequences of incorporating gradual changes in foraging success were the pauses in singing after dawn and before dusk. Because these pauses are unexpected, a robust prediction, and not predicted by the rival theory, the best test of Explanation 2 may be whether such pauses have been observed empirically (Roberts & Pashler 2000).

There is anecdotal evidence of pauses following the dawn chorus. For instance, in Ipswich sparrows, *Passerculus sandwichensis princeps*, the dawn chorus is followed by such a complete silence that Reid (1987; and personal communication) was misled into studying the later recommencement of song, thinking that this was the dawn chorus! However, the published singing routine most convincingly fitting my model is for red jungle fowl, *Gallus gallus*, the progenitor of domestic poultry (Collias & Collias 1967). A double peak in the dawn chorus, with less crowing in between, appeared not only in a routine that averages the output of many birds over several days but also in the two other figures that are records for individual days. Collias & Collias explained the two peaks in terms of the second occurring after relocation from the roost to water holes. If foraging occurs only away from the roost, this explanation for the pause may be compatible with mine. Unfortunately, quantitative data on when birds foraged are lacking in their study, and are generally rarely collected in the field because foraging is more difficult to monitor than singing. Another data set that

fairly consistently suggests a temporary lull after the dawn chorus is for the chaffinch, *Fringilla coelebs* (Klockars 1941). And lekking black grouse, *Tetrao tetrix*, consistently stop displaying for half an hour over sunrise (Koivisto 1965).

Few published singing routines deal with the dusk chorus, but even with the dawn chorus it is hard to judge how typical a pause is, because the data are rarely presented and/or collected in a suitable form. One problem is temporal resolution: figures often plot the song output summed over long time intervals, such as an hour. My models predict briefer pauses than this, which thus may not stand out if averaged with periods of full song. It would be better to use shorter time intervals and to plot the data not as a bar chart but as a continuous curve showing the average over a moving time window. This may be impossible for data based on discontinuous sampling, which may be necessary to monitor more than one individual each morning.

Some published routines showing an appropriate pause (e.g. that for yellow warbler, *Dendroica petechia*, in Staicer et al. 1996) are for single birds on individual days. With such data, one expects pauses to arise through chance events such as a run of bad luck foraging, a rain shower, or some social interaction. Averaging over the several individuals within earshot on a single day need not overcome this problem, because they may be responding to the same weather conditions and because each individual may be stimulating the others to sing. It is also possible that different individuals have different routines, for instance because of a different pairing status: averaging one individual with another that has a dawn chorus an hour later will produce two peaks in the average routine, even though neither individual showed a double peak.

For this reason, it might be best to report the average routine for an individual followed over a few consecutive days, rather than averaging over individuals. However, averaging over days can also introduce artefacts. For instance, if the dawn chorus starts later on cloudy days, an average over fine and cloudy days may produce two peaks, even though no such double peak occurred on any one day. Conversely, a pause could occur every day, but if the start of the dawn chorus varies between days, the smoothing effect of averaging could obscure the pause. Perhaps a better approach to averaging days is to average time intervals which are the same time after the commencement of that day's dawn chorus.

Even if empirical routines do show a pause after the dawn chorus and before the dusk chorus, there unfortunately are explanations other than gradual changes in foraging success. One example is Brown's (1963) explanation for why willow warblers, *Phylloscopus trochilus*, may sing for 3–4 min early in the morning, then fall silent for 20 min, before recommencing at sunrise: that they fall silent to avoid competing with the dawn chorus of the chiffchaff, *P. collybita*. More generally, an obvious reason for a pause is that birds are resting after the intense singing activity of the dawn chorus or in preparation for the dusk chorus. This explanation begs the question of why singing goes on so long and continuously at dawn

and dusk that birds need a long rest. Why not sing and rest for shorter times and more often, in which case no period would exhibit a consistent or prolonged pause? Explanation 2 provides one reason, but Hutchinson et al. (1993) identified another advantage in singing continuously for long periods rather than for the same total period but in short bursts. Their model showed that females choosing males able to sing in long continuous bouts selected better-quality mates, so that sexual selection should favour long bouts. The routines that were optimal when long bouts were advantageous could indeed exhibit two or even three peaks in song output over the morning, although selection for still longer bouts led to a single long bout of dawn singing.

Given these problems, a better approach to investigating the influence of gradual changes in foraging success may be to manipulate light intensities in an aviary. Then it would be easier to quantify how foraging success depends on light intensity, so that the model's parameter values could be fitted to the exact situation faced by the birds. Besides monitoring song output, one might use a balance on the feeder to monitor fat levels, enabling the policy as well as the routine to be measured (Hutchinson & McNamara 2000).

However, a bird may respond in various plausible ways to manipulations of the light regime. Figure 7 shows two possible responses to a one-off sudden increase of light levels at first light, after which foraging success is consistent throughout that morning. I assume that birds are adapted to the light regime in Fig. 2a, and one possibility is that their policy at each time of day remains unchanged; then our manipulation of foraging success has little effect on the routine (Fig. 7a). Alternatively, birds might use light levels as a cue to time of day, so that bright light at dawn would fool birds into using the policy appropriate for midmorning. The effect on the routine is much more dramatic (Fig. 7b). In fact, birds should be adapted to respond to short-term changes in food availability caused by factors other than light, so both predictions may be too simplistic.

Now suppose that, rather than a one-off manipulation, we trained birds over many days to a novel light regime. We might predict that the policy would adjust to be optimal to the new regime. Alternatively, however, the response might be the same as for a one-off manipulation, because natural selection could have hardwired the policy into the bird's neuronal and hormonal physiology. Or the policy might adjust to an intermediate extent. If the policy does adjust, there is again the question of whether adjustment is in direct response to the changed pattern of food availability, or whether birds are using light levels as a cue to the time of day and are hardwired to predict present and future food availabilities according to how they relate to time of day in the wild. Light levels predict not only foraging success, but such relevant factors as the ease of detecting intruders or predators and the availability and fertility of females. To detect whether it is foraging success that is important, we might compare the response to two food sources, one that is harder to feed on in poor illumination, and another that is equally available then (e.g. a dish of

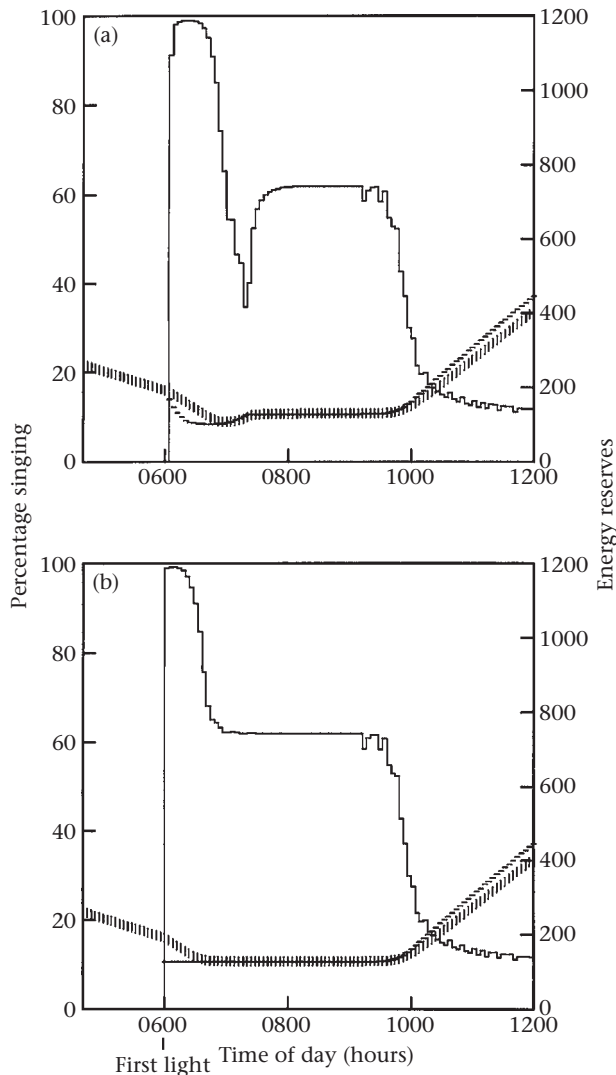


Figure 7. Two ways in which a bird with the optimal routine in Fig. 2a might respond to a one-off sudden increase in light at first light that increases foraging success to midday levels. Only the first half of the day is shown. (a) The policy remains the same with respect to time of day. (b) The bird uses the policy appropriate for mid-morning from first light onwards.

mealworms with and without some material for them to hide in). An alternative approach is to use an operant technique to manipulate food availability on a regular daily cycle independent of light levels. Not changing light intensity also avoids the possibility that the bird interprets different light regimes as indicating different times of year. Directly manipulating foraging success was the approach taken by Mace (1989a) in investigating this problem, but her changes in foraging success were sharp and appeared not to influence the singing routine.

I have concentrated on only two of the many explanations for why birds sing more at dawn and dusk. When the model was adjusted to incorporate some other explanations, the predicted routines were similar (Fig. 4). In general, the dawn chorus provides a problem with too many potential solutions. Some explanations, such as

Explanation 2 and the acoustic transmission hypothesis, depend on special environmental conditions at dawn or dusk. Other explanations depend merely on there being two parts of the day, and what is special about dawn and dusk is then not the environmental conditions themselves but that one part of the day has ended and the other is starting. Explanation 1 is one example, and others are the ideas that vacant territories or available mates accumulate overnight. Unfortunately, with both types of explanation, many such factors change in concert, and in any species a different set of factors could have selected for similar observed routines. Furthermore, factors other than those important as ultimate causes may be used as proximate cues for when to sing. The optimality models in this paper have allowed us to isolate the evolutionary consequences of each explanation and each environmental factor, and to examine proximate responses separately from evolutionary responses. Disentangling the influences of the different ultimate explanations empirically, by means of comparative analyses or experimental manipulations, will not be so straightforward.

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References

- Avery, M. I. & Krebs, J. R. 1984. Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis*, **126**, 33–38.
- Bakken, G. S., Murphy, M. T. & Erskine, D. J. 1991. The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. *Physiological Zoology*, **64**, 1023–1049.
- Birkhead, T. R., Cunningham, E. J. A. & Cheng, K. M. 1996. The insemination window provides a distorted view of sperm competition in birds. *Proceedings of the Royal Society of London, Series B*, **263**, 1187–1192.
- Brown, R. G. B. 1963. The behavior of the willow warbler *Phylloscopus trochilus* in continuous daylight. *Ibis*, **105**, 63–75.
- Collias, N. E. & Collias, E. C. 1967. A field study of the red jungle fowl in north-central India. *Condor*, **69**, 360–386.
- Dabelsteen, T. & Mathevon, N. 2002. Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. *Acta Ethologica*, **4**, 65–72.
- Endler, J. A. 1993. The color of light in forests and its implications. *Ecological Monographs*, **63**, 1–27.
- Godfrey, J. D. & Bryant, D. M. 2000. State-dependent behaviour and energy expenditure: an experimental study of European robins in winter territories. *Journal of Animal Ecology*, **69**, 301–313.
- Houston, A. I. & McNamara, J. M. 1987. Singing to attract a mate: a stochastic dynamic game. *Journal of Theoretical Biology*, **129**, 57–68.
- Houston, A. I. & McNamara, J. M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Hutchinson, J. M. C. & McNamara, J. M. 2000. Ways to test stochastic dynamic programming models empirically. *Animal Behaviour*, **59**, 665–676.

- Hutchinson, J. M. C., McNamara, J. M. & Cuthill, I. C. 1993. Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour*, **45**, 1153–1177.
- Kacelnik, A. 1979. The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Animal Behaviour*, **27**, 237–242.
- Kirk, J. T. O. 1983. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge: Cambridge University Press.
- Klockars, B. 1941. Studier över fågelsångens dagsrytmik. *Ornis Fennica*, **18**, 73–110.
- Koivisto, I. 1965. Behavior of the black grouse, *Lyrurus tetrix* (L.) during the spring display. *Finnish Game Research*, **26**, 1–60.
- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica*, **18**, 216–226.
- Leopold, A. & Eynon, A. E. 1961. Avian daybreak and evening song in relation to time and light intensity. *Condor*, **63**, 269–293.
- Mace, R. 1986. Importance of female behaviour in the dawn chorus. *Animal Behaviour*, **34**, 621–622.
- Mace, R. 1987. Why do birds sing at dawn? *Ardea*, **75**, 123–132.
- Mace, R. 1989a. The relationship between daily routines of singing and foraging: an experiment on captive great tits *Parus major*. *Ibis*, **131**, 415–420.
- Mace, R. 1989b. A comparison of great tits' (*Parus major*) use of time in different daylengths at three European sites. *Journal of Animal Ecology*, **58**, 143–151.
- McNamara, J. M., Mace, R. H. & Houston, A. I. 1987. Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology*, **20**, 399–405.
- Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, New Jersey: Princeton University Press.
- Otter, K. & Ratcliffe, L. 1993. Changes in singing behavior of male black-capped chickadees (*Parus atricapillus*) following mate removal. *Behavioral Ecology and Sociobiology*, **33**, 409–414.
- Reid, M. L. 1987. Costliness and reliability in the singing vigour of Ipswich sparrows. *Animal Behaviour*, **35**, 1735–1743.
- Roberts, S. & Pashler, H. 2000. How persuasive is a good fit? A comment on theory testing. *Psychological Review*, **107**, 358–367.
- Slagsvold, T. 1996. Dawn and dusk singing of male American robins in relation to female behavior. *Wilson Bulletin*, **108**, 507–515.
- Slagsvold, T., Dale, S. & Sætre, G-P. 1994. Dawn singing in the great tit (*Parus major*): mate attracting, mate guarding, or territorial defence? *Behaviour*, **131**, 115–138.
- Staicer, C. A., Spector, D. A. & Horn, A. I. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 426–453. Ithaca, New York: Cornell University Press.
- Thomas, R. J. 1997. Functions of daily singing routines in birds. D.Phil. thesis, University of Sussex.
- Thomas, R. J. 1999a. Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Animal Behaviour*, **57**, 277–284.
- Thomas, R. J. 1999b. The effect of variability in the food supply on the daily singing routines of European robins: a test of a stochastic dynamic programming model. *Animal Behaviour*, **57**, 365–369.
- Thomas, R. J. & Cuthill, I. C. 2002. Body mass regulation and the daily singing routines of European robins. *Animal Behaviour*, **63**, 285–292.
- Thomas, R. J., Appleby, B. M., Appleyard, N. J. & Morecroft, M. D. In press. Testing hypotheses about daily singing routines using nocturnal singers. *Behavioral Ecology*.
- Welling, P., Koivula, K. & Markku, O. 1997. Dawn chorus and female behaviour in the willow tit *Parus montanus*. *Ibis*, **139**, 1–3.
- Witter, M. S. & Cuthill, I. C. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 73–92.

Appendix

This appendix details the model used to generate Fig. 1a (i.e. with overnight stochasticity and step-function changes in the rewards from foraging and singing). Alterations to this baseline model are explained in the text and figure captions.

Day and night periods are each made up of 180 time intervals, with sudden transitions at 0600 and 1800 hours. At night birds must rest; during the day they may sing, forage or rest. The metabolic cost of each activity depletes energy reserves: a bird with reserves i at time t that then sings will have $i - d_s(i) - B_s$ reserves at time $t+1$. Here the reserve-dependent component $d_s(i) = S_0 + S_1 i + S_2 i^2$. The stochastic component $B_s = -\eta_s$ or η_s , each with probability $(1 - q_s)/2$, or $B_s = 0$ with probability q_s . Corresponding parameters for foraging and resting are indicated by replacing the letter s with f or r ; thus with foraging $d_f(i) = F_0 + F_1 i + F_2 i^2$. In contrast, metabolic expenditure whilst resting is independent of reserves and at night has an extra source of between-night stochasticity: in a proportion q_{temp} of nights $d_r(i) = R_{\text{normal}}$, otherwise $d_r(i) = R_{\text{cold}}$. During daytime, $d_r(i) = R_{\text{normal}}$. A foraging bird always pays the metabolic cost, but has probability p_{food} of additionally gaining e energy units. For technical reasons associated with the dynamic programming algorithm, at each time step reserves are converted onto an integer scale using linear interpolation (an extra source of stochasticity). Thus, if reserves after metabolic expenditure and food gain are x , they become $[x]$ with probability $1 + [x] - x$, and $[x] + 1$ with probability $x - [x]$, where $[x]$ denotes the integer part of x . If reserves fall to ≤ 0 , the bird has starved to death.

If a bird sings, it has probability p_{pair} of pairing in that time interval. Once paired it remains paired, so it no longer sings. Performance is judged at the end of a time window with a constant probability of terminating at each time step; expected window length = 10 days. The terminal reward is 0 if dead, and otherwise 1 if unpaired, or 2 if paired.

Dynamic programming (Houston & McNamara 1999) finds the policy maximizing this expected terminal reward, working backwards until policies and the expected terminal reward converge. Routines are found by following a population forward in time until convergence in the distribution of states at dusk. When working forward, night temperatures were always normal. But after convergence, I could take the distribution of reserves at dusk as a starting point, and then introduce a single night of different temperature or duration.

Baseline parameter values are: $e = 32$, $p_{\text{food}} = 0.7$, $S_0 = 7$, $S_1 = 10^{-3}$, $S_2 = 10^{-6}$, $\eta_s = 3.5$, $q_s = 0.5$, $F_0 = 10.5$, $F_1 = 2 \times 10^{-3}$, $F_2 = 2 \times 10^{-6}$, $\eta_f = 6.2$, $q_f = 0.5$, $R_{\text{cold}} = 4.2$, $R_{\text{normal}} = 3.5$, $q_{\text{temp}} = 0.9$, $\eta_r = 0.8$, $q_r = 0.5$, $p_{\text{pair}} = 0.002$. Energy units are arbitrary.