Song, sexual selection, starvation and strategic handicaps

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Abstract. Peaks in song output at twilight, particularly dawn, are typical of many birds. Recent attention has focused on the honesty of male advertisement, and on whether dawn is a particularly good time for females to assess male quality. In the present model a male divides his times between singing and feeding. If he sings more he is more likely to starve. A natural outcome is that song acts as a strategic handicap and as an honest signal of male quality. By using stochastic dynamic programming, diurnal variation in female assessment is shown to have a profound influence on male daily routines, but dawn is rarely the best time for assessment of quality. Females do not much enhance their probability of pairing with a high-quality male by varying responsiveness to song with time of day; constraints on female time budgets probably have more influence on the timing of male song than does optimization of quality discrimination. But females do greatly enhance their discriminatory efficiency by remembering past song output (song is then more concentrated at certain times, particularly morning, and males may even remain silent on alternate days). In general, the harder the task demanded of a male, the more efficient is the female rule in discriminating male quality.

In a wide variety of contexts a state-dependent and game-theoretical approach is required to understand behaviour. In the case of mate choice a male's optimal state-dependent strategy may depend on his own phenotype, the strategies adopted by other competing males and the strategies adopted by females. Similarly, a female's optimal strategy depends on her phenotype and the strategies of other females and of males. In this paper we focus just on the co-adaptation between the strategies of opposite sexes. Males differ in quality and each male attempts to maximize his probability of both pairing and survival. Females discriminate quality only on the basis of when and how often males display. We seek female strategies that perform well when male strategies are optimally adapted to that particular female strategy.

The time and effort that a male allocates to display is allowed to depend on the time of day and energy reserves. Following such a strategy leads to a stable routine. These routines, rather than the underlying strategies, are the focus of this paper. Because different activities compete for energy as well as time, the optimal daily routine is an adaptive compromise that need not be a simple reflection of diurnal changes in external factors such as light,

food availability, or predation risk. A particularly clear example is bird song: singing demands energy, yet time spent foraging reduces song output. In addition to fuelling song, energy reserves are a buffer against the risk of starvation, so the allocation of time to singing versus feeding is a compromise that must take into account overnight energy requirements as well as those during the day.

There are several reasons why diurnal variation in bird song is an attractive system in which to investigate the function of daily routines. First, at least 15 explanations have been proposed for the 'dawn chorus' that is characteristic of most species (reviews in Kacelnik & Krebs 1982; Mace 1987; Cuthill & Macdonald 1990). However, few papers present clear null hypotheses against which to assess the putative impact of any one factor on an animal's time budget. Thus there is a need for formal modelling. Second, the phenomenon is amenable to this approach as it is not unrealistic to characterize the daily activity of many, particularly unpaired, male birds as consisting of just two activities, singing and feeding (Searcy & Andersson 1986), with song serving to attract mates (Eriksson & Wallin 1986). Third, information on singing activity is probably easier to collect than many time-budget data, making

predictions testable. Lastly, as bird song increases mating opportunity at the expense of survival, we gain an insight, not just on the trade-off between two activities but also on the interaction between sexual and natural selection.

Because the probability of starvation varies with energy reserves, and these are affected by what the bird does (e.g. foraging versus singing versus resting), the problem of optimal daily routines lends itself to stochastic dynamic programming (McNamara & Houston 1986; Mangel & Clark 1988). We follow the approach of McNamara et al. (1987), who modelled daily routines of singing, but with several important modifications. McNamara et al. investigated the optimal policies of identical males, whereas we incorporate differences in male quality. This allows us to investigate the efficiency with which females can discriminate between males of different quality by using choice rules based on song output. For example, because song may be more costly at some times of day than others, some times of day may be better for discriminating between males (e.g. Garson 1978; R. D. Montgomerie 1985, abstract of a paper presented at the 19th International Ethological Congress, Toulouse, Vol. 1, page 242). However, since the optimal male routine depends on the female rule, and vice versa, the success of different female rules may not be obvious. Our strategy is as follows. First, we allow the females' response to song to vary with either time of day or memory of past male song output. Second, for a given female decision rule we find the optimal singing routines for each male. Lastly, we assess the efficiency of the female rule at discriminating, via their song, between males of different quality. A limitation is that we do not consider intra-sexual competition for mates, which will determine which strategies are evolutionarily stable.

The dependence of optimal male singing policy on the female decision rule, and of the optimal female decision rule on the male policy, leads to some counter-intuitive results discernible only through formal modelling. This allows us to reject some previous explanations for the dawn chorus and delimit the conditions under which others may apply. More generally, our models illuminate how song operates as a strategic handicap (Grafen 1990a, b), conveying honest information about male, or territory, quality.

We begin by analysing male routines when male song is equally likely to attract a mate at any time during the daylight period. We then consider more sophisticated rules of female choice: first, females may prefer song at a particular time of day; second, they may prefer continuous bouts of singing. In the Discussion we consider the limitations of our model and extend its application, for instance to other functions of bird song and to the displays of other animals. Finally, we briefly consider how our model may be tested in the field.

## CONSTANT PAIRING PROPENSITY

In this section we find optimal daily routines for a simple model based on that of McNamara et al. (1987). (Later we treat more complex models using the same approach.) We first give a verbal description of the model, deferring a precise mathematical description to the Appendix. We then discuss the model's predictions for one set of parameter values. Taking these values as a baseline we subsequently perform a sensitivity analysis which investigates the effect of changing environmental and physiological parameters on the predicted routine.

The Model

A male's state is characterized by his energy reserves and whether he has paired. There is no predation but birds die if their energy reserves fall to zero. How energy reserves change with time depends on the actions chosen. Every day is divided into a daylight period followed by night. Daylight and night are of equal length and each is subdivided into 75 time intervals. During a daylight interval an unpaired male either sings, forages or rests. Males cannot feed at night. Since males also cannot pair at night, in our simple model they rest.

Pairing propensity

A male can obtain a mate only by singing. We call the probability that a singing male obtains a mate within one time interval the pairing propensity. In this section the pairing propensity is constant throughout the daylight period. This could arise, for example, if females arrived in the pairing area at a random time and chose the first male who sang. Males pair at most once. Having paired, a male no longer sings, but still needs to forage to avoid starvation.
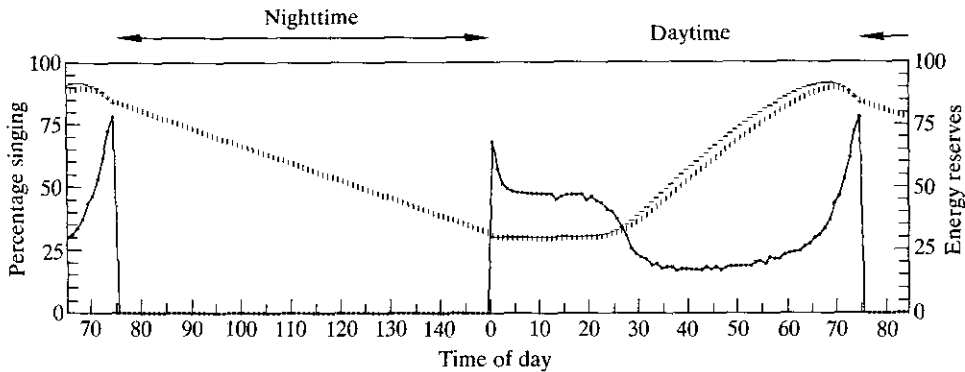
Figure 1. Policy and routines from the baseline model given in the text. (-), indicate the switchpoint in reserves below which a bird should feed instead of sing; they should never sing at night. (|), show the mean of the resultant distribution of reserves. The connected dots show the percentage of the population in song; when reserves lie mostly above the switchpoint, song output is highest. The small blips in the singing routine are an artefact caused by modelling reserves and time as discrete values. Each 24-h period is divided into 150 equal time intervals numbered from dawn. In subsequent figures parameter values are as in the baseline model, unless otherwise stated.

Food gained

If the bird forages during a time interval he may or may not find a food patch. If he fails to find a patch he obtains no food. All patches yield the same food reward. The mean and variance in the amount of food obtained during a time interval thus depend on the probability a patch is found and on the amount within a patch. Singing or resting birds find no food.

Metabolic expenditure

The mean metabolic expenditure of the three activities differ. Foraging and singing use more energy than resting, and in the baseline model foraging more than singing.

In nature being too fat has at least two potential costs: fat birds are more prone to predation, and they use more energy when active, especially when in flight (Norberg 1981; Witter & Cuthill, in press). In our model, for simplicity, all the cost is represented by an increase in metabolic expenditure with energy reserves. This rate of increase we refer to as the metabolic slope.

There is stochasticity in metabolic expenditure, although this is small in comparison with stochasticity in the food supply. Temperature variations during the day are ignored. Overnight temperature varies from night to night and there are occasionally very cold nights. Resting metabolics increase with decreasing temperature.

The pairing window

There is a 'pairing window' during which males can pair. We assume that if the pairing window has not ended by the beginning of a time interval the probability that it ends during the interval is a small constant. The window consequently has exponential length. We have chosen the termination probability so that the mean window length is 5 days.

The terminal reward

At the end of the pairing window we assign a reward of 1 to unpaired males and 2 to paired males. Males that have starved receive 0 reward. These numbers are arbitrary, but McNamara et al. (1987) showed that routines are very robust to changes in the rewards provided that paired birds get a higher reward than unpaired.

Optimal policies

The optimal policy specifies the action a male should choose as a function of his energy reserves and the time of day. Because the pairing window has exponential length the policy is the same each day. In our computations it is never optimal to rest during daylight. There is a critical level of reserves below which it is optimal to forage and above which it is optimal to sing. (These results do not always hold in the 'memory' model given below.) This switchpoint depends on time of day. Figure 1 shows

the optimal policy for the baseline parameter values given in the Appendix. We now discuss features of this policy and of the resulting daily routine.

The Baseline Daily Routine

A large population of males independently following the same policy quickly settles down to an equilibrium routine in which the proportion of unpaired males singing at a given time of day is the same each day. The equilibrium proportion changes with time of day and it is these equilibrium daily routines that we present in this paper. We also calculate the probability that a male following the routine pairs within a day (which we term 'pairing success') and the probability that the male dies of starvation.

Figure 1 gives the daily routine that results from following the optimal baseline policy. The routine exhibits features that occur over a wide range of parameter settings. As in the similar model of McNamara et al. (1987) there are four key features: (1) singing levels are very high at dawn (the dawn chorus), followed by (2) a plateau of moderately high song output during the morning, then (3) an afternoon dip and (4) a final dusk chorus. We now explain why these patterns arise.

Energy reserves at dusk enable a bird to survive the night, when feeding is impossible, and still have enough reserves at dawn to withstand an unlucky run of feeding attempts. In order almost to eliminate the possibility of starvation, birds budget for an unusually cold night. If the night is not that cold, reserves at dawn lie above the switchpoint and birds sing until reserves drop to the switchpoint. This generates the dawn chorus.

The switchpoint in reserves is constant during the first part of the day. The level of the switchpoint is an optimal compromise. Raising the switchpoint would reduce the probability of starvation during the day. But the advantage of doing so is outweighed by the importance of singing before the pairing window ends, and because mass dependence of metabolic costs means that more food is required to maintain reserves at a higher level. As reserves drop to the switchpoint the dawn chorus ends and an equilibrium is reached in which birds alternate between foraging and singing while keeping reserve levels around the constant switchpoint. This produces the morning plateau in song.

There is a target level of reserves which birds aim to achieve by dusk. The switchpoint rises to meet this level after the morning plateau and birds following the policy decrease their song output as they build up reserves. This gives rise to the afternoon dip.

Since the food supply is stochastic, birds play safe and start to build up reserves sooner than they would need with a deterministic food source. Consequently they usually achieve their target before dusk and can recommence singing. This is the dusk chorus.

Variations on the Baseline Model

We have carried out an extensive search of parameter space to see how routines change as environmental and physiological parameters vary. This is important for several reasons (see also Gladstein et al. 1991; Houston et al. 1992).

(1) Observing the effect of parameter changes helps us to understand the mechanisms that give rise to the routines, the role individual components play and the interaction between components.
(2) One could have confidence in the model as a predictor of natural routines only if predicted routines were robust to changes in parameters whose true values are only approximately known.
(3) McNamara et al. (1987) carried out a search of parameter space with their model and concluded that routines were robust. Our analysis is both more systematic and allows a wider variation in parameter values. While agreeing that the baseline routine is robust, we have identified extreme parameter values which give qualitatively different routines. Variation in parameter values may account for some of the diversity of natural routines, and we make testable predictions about when certain routines should occur.
(4) These qualitatively different routines play an important role in the next section where we analyse time-of-day variation in pairing propensity.

We now summarize the effects of altering parameter values.

Variability in overnight energy expenditure

This arises mainly because of unpredictable changes in temperature and will be greater when nights are longer. As observed by McNamara et al. (1987), a reduction in variability reduces the dawn chorus. This is because birds need not budget for such an unusually cold night, so after a normal
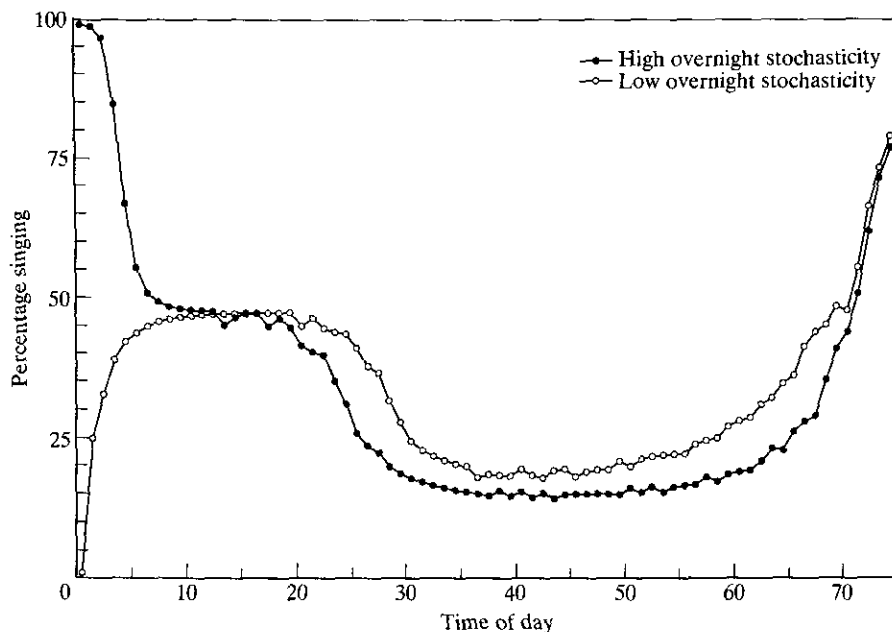
Figure 2. The effect of severity of the occasional cold night on the singing routine. In the baseline routine (Fig. 1) a cold night requires $R_{cold} = 3.6$ energy units per time interval ($R_{normal} = 2.8$); ●: $R_{cold} = 4.2$; ○: $R_{cold} = 3.0$.

night they have less surplus energy at dawn. What McNamara et al. did not observe is that if overnight variability is very low the dawn chorus can be replaced by singing levels even lower than the plateau, provided that the metabolic slope of foraging is sufficiently high (Fig. 2).

Mass-dependent metabolism

The rate at which metabolic costs increase with energy reserves (metabolic slopes) has a strong influence on the dusk chorus, which is otherwise the most stable feature of our model. What matter are the relative magnitudes of the metabolic slopes of singing and foraging. When that for singing is relatively high, dusk song is penalized by high reserves at this time. Instead of singing, birds at dusk store up energy to sing more at dawn when body mass is low (Fig. 3). Conversely, when the metabolic slope of foraging is relatively high, birds sing less at dawn (Fig. 3).
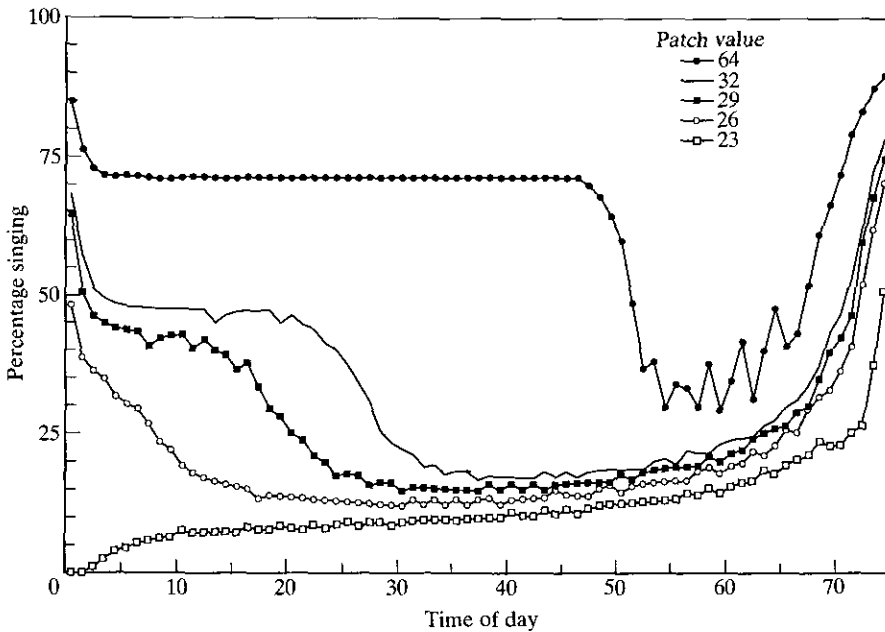
Energy availability

There are several ways in which we can lower the available energy: by decreasing the daylight hours, the probability of finding a food patch while foraging, or the food per patch, or by increasing the metabolic costs of all or some activities. Increasing the metabolic cost of singing reduces singing levels throughout the day, but especially at dusk, with levels at dawn remaining relatively stable. All other alterations to the available energy change the routine in ways similar to one another, but different to when the cost of singing is altered. These effects are illustrated in Fig. 4. The dusk chorus and afternoon dip are little altered by a reduction in the available energy (patch value 29 in Fig. 4) but the birds start to accumulate their dusk reserves earlier, so the length of the plateau is reduced. Conversely, the main consequence of increasing the available energy (patch value 64) is to prolong the plateau. Under severe reductions in the available energy the build up of reserves begins so early that the morning plateau disappears altogether. Sometimes the dawn chorus falls directly to the dip previously characteristic of the afternoon (patch value 26); or sometimes the dawn chorus is itself reduced so that the plateau is replaced by a rounded peak in the early morning (not illustrated). With even greater severity, singing may increase throughout the day to a relatively unaffected dusk chorus (patch value 23).
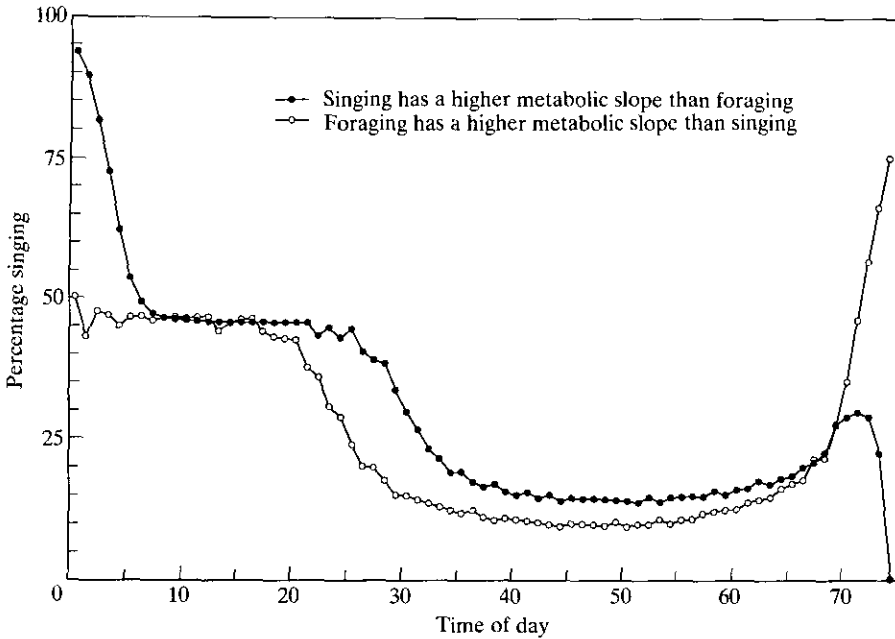
Figure 3. The effect of the relative metabolic slopes of singing and feeding on the relative magnitude of dawn and dusk choruses. ●: The quadratic term for the metabolic cost of singing (S_2) is 10 times that for feeding (F_2) and the linear terms are equal $(S_1 = F_1 = 2 \times 10^{-3}, S_2 = 5 \times 10^{-5}, F_2 = 5 \times 10^{-6})$. ○: No metabolic slope for singing and the quadratic term for feeding is 10 times that in the baseline model $(S_1 = S_2 = 0, F_1 = 2 \times 10^{-3}, F_2 = 5 \times 10^{-5})$.

Figure 4. The effect of energy availability on singing routine. The energy value of a food patch (e) is manipulated here. Other manipulations of energy availability have qualitatively similar consequences.
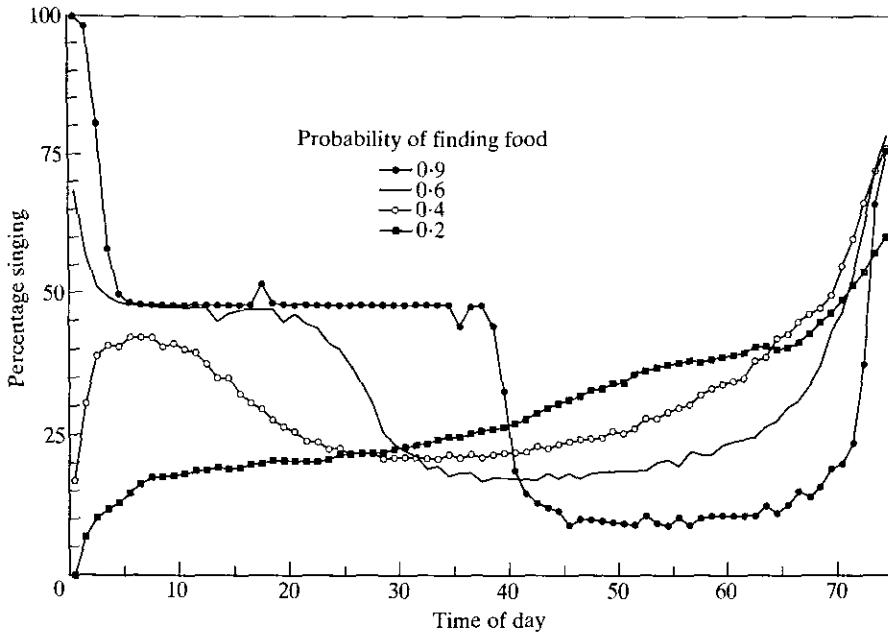
Figure 5. The effect of the stochasticity of energy supply on the singing routine. The probability of the bird finding a food patch (p_{food}) is altered here; the value of the patch (e) is also adjusted so that the mean food gain stays constant (19·2 per time interval).

Feeding stochasticity

If the variability of the food supply is increased while keeping the mean rate of gain while foraging constant, there are two main effects on routines (see Fig. 5). Since food is less certain, birds need to build up reserves earlier in the day and they reach their dusk target reserves earlier. They then sing, so the dusk chorus starts earlier. The effect earlier in the day is similar to the effect of reducing available energy.

MALE QUALITY AND FEMALE CHOICE

Introduction

The metabolic energy required to perform an activity may be related to a bird's quality. For instance one expects expenditure to be high if parasite load is high, or if the condition of flight feathers or of insulation is poor. The amount of food a foraging bird finds within a given time may also indicate quality. Birds that find a lot may be more efficient searchers or may hold better territories (Gottlander 1987). It is advantageous to females to pair with a high-quality male, either because the male has better genes or because he (or his territory) may be better able to feed the young. Since the amount of singing a male bird can perform, and hence his quality, increases with the spare energy available, females should use song as a means to choose the highest-quality male.

To investigate this idea we consider three types of males, referred to as individuals of high, intermediate and low quality, whose metabolic expenditures are low, medium and high, respectively. Table I illustrates the performance of individuals of each type. In this example, and in other manipulations of male quality (see e.g. Table II), we have found that (1) pairing success (proportional to song output) increases with male quality, and (2) starvation probability decreases with male quality, and hence (3) expected terminal reward increases with male quality. We know that song will act as a handicap in that singing will increase the chance of death by starvation. What (1) and (3) show is that it is optimal to use song as a strategic handicap (as envisaged by Grafen 1990a, b). It is not optimal for low-quality males to sing as much as high-quality males because if they did the increase in starvation would more than counteract the increase in fitness due to increased

Table I. Fitness consequences of quality for males; manipulations of the metabolic costs of singing and foraging (S_0, F_0)

Quality	S_0	F_0	% Paired	% Starved	Fitness
Low	9	13	8·32	0·070	1·311
Baseline	8	12	9·60	0·052	1·347
High	7	11	10·85	0·040	1·380

For each parameter value we find the optimal policy and then, in a population following this policy for a long time, *we calculate the percentage pairing and starving within a day.* The percentage paired directly reflects the proportion of time spent singing. Fitness is the mean terminal reward. Discrimination Indices presented in this paper are based on this particular manipulation. Here the Discrimination Index (DI) = 10·85/8·32 = 1·3029 (without standardizing baseline pairing success at 10%).

Table II. Fitness consequences of quality for males: manipulation of the energy value of a food patch (e)

Quality	e	% Paired	% Starved	Fitness
Low	20	2·82	0·285	0·846
	23	3·45	0·278	1·128
	26	5·98	0·107	1·234
	29	7·99	0·070	1·301
Baseline	32	9·60	0·052	1·347
	35	10·94	0·042	1·382
	38	12·07	0·034	1·409
	41	13·04	0·029	1·430
	44	13·88	0·026	1·448
High	64	17·52	0·015	1·514

See legend to Table I.

pairing. The possibility of starvation thus causes *song to be an honest advertisement of male quality.*

We defined pairing propensity to be the probability that a singing male pairs in one time interval. *It seems probable that pairing propensities* in the wild are affected by the behaviour of other males, and in particular by the number of other *males singing at the same time. For the moment we* ignore this possibility, treating a male as if he were solitary, and suppose that pairing propensity *depends entirely on the choice rule employed by* females. In analysing the baseline model we took pairing propensity to be a constant during daylight. But this form of pairing propensity may not be the best female strategy if females wish to maximize

their chances of pairing with a high quality male. In this section we investigate whether more sophisticated female behaviour can do better. Three classes of female strategy are considered.

(1) Constant pairing propensity. Here we alter the level of pairing propensity.
(2) Time-dependent pairing propensity. Here we allow pairing propensity to depend on time of day.
(3) Female memory. Female choice is allowed to depend on measures of how much singing a male has performed previously.

To quantify how good a female's strategy is at selecting high-quality males we introduce the Discrimination Index (DI), defined as

$$DI = \frac{\text{Probability a high-quality male pairs over 1 day}}{\text{Probability a low-quality male pairs over 1 day}}.$$

One would expect female behaviour to evolve so that females have high DIs, so we look for rules *within each class that maximize DI. In calculating* DI we assume that male behaviour has evolved so that individual males are optimal given female *behaviour. Thus, the routines that we are interested* in finding are optimal male routines for high-DI female strategies.

Although we have taken male quality as synonymous with low metabolic expenditure, we obtain the same qualitative results as those below if *quality is taken as synonymous with the ability to* obtain food.

Constant Pairing Propensity

Here, we consider the effect of varying the level *of pairing propensity while keeping pairing* propensity the same in each time interval.

The singing routine is little affected by even large *changes in pairing propensity. Although DI is also* little affected the trend is that DI increases as pairing propensity decreases (Table III).

Time-dependent Pairing Propensity

The baseline male singing routine has a mid-morning plateau of song (Fig. 1). Under moderate changes in the availability of energy *the main change in the routine is a change in the* length of this plateau (Fig. 4). Low-quality males

Table III. Effect of a decrease in the probability of a female pairing with a singing male in each time interval (p_{pair})

p_{pair}	% Paired	DI
0·004	9·602	1·304
0·0004	0·987	1·337
0·00004	0·097	1·363

The number of intermediate-quality males paired each day decreases, but DI increases.

have a shorter plateau, so when they stop only higher-quality males will still be singing. Intuition would suggest that this is a particularly good time for females to choose mates, and hence that a high pairing propensity at this time should result in a high DI. It is a purpose of this paper to show that such reasoning is incorrect. The reason is that, once the female choice rule changes, so does the optimal male routine. In this example it changes dramatically (see top left of Fig. 7a). Birds delay singing until the female pairing propensity is high and so even low quality males have sufficient energy to sing in the late morning. Whether this alteration to pairing propensity raises or lowers DI depends on the factor by which pairing propensity changes.

The above example shows the danger of naively using intuitive ideas about daily routines, and shows the need for a formal model. We now use our model to investigate systematically the effect of time-of-day variation in pairing propensity.

Methods

Each of the 75 steps in the daytime could have a different pairing propensity, but it is not feasible to try all possibilities. Our strategy is to divide the daylight hours into three blocks. Pairing propensity is constant within each block. Over the first and third blocks the pairing propensity is the same. Over the middle block it is either 0·5, 0·95, 1/0·95 or 2 times as likely. The lengths of the first and third blocks are varied in steps of 5 units, and for each combination of block lengths DI is calculated (Fig. 6).

To check for artefacts created by sudden, step-wise transitions in pairing propensity, we also consider more gradual transitions, in which the change in pairing propensity between the central block and dawn or dusk follows a cubic spline.

DI depends on both the relative levels of pairing propensity during a day and on the absolute levels. As shown above, DI increases as the absolute level decreases. To standardize for the effect of absolute level we adjust this level so that an intermediate-quality male following his optimal routine has probability 0·1 of pairing on each day.

Routines

Before observing which patterns of pairing propensity improve DI most, we consider the routines generated. A reduction of pairing propensity by a half is quite sufficient to stop almost all song in that portion of the day, even when that leaves less than half of the daytime in which to sing (Fig. 7b). In contrast a reduction in pairing propensity to 0·95 of the value elsewhere does not cause silence for long (Fig. 7a), although it still alters the routine dramatically. When this 5% reduction in pairing propensity occurs from the start of the day, a double dawn chorus occurs, the first occurring at dawn as before, and the second generated by a tendency to hold on to reserves until the female pairing propensity increases (Fig. 7a). Similarly a reduction in pairing propensity at the end of the day generates a double dusk chorus (Fig. 7a). A gradual transition in pairing propensity, modelled with a cubic spline, tends to smooth out such double choruses, although not always completely. Making pairing propensity change even more smoothly, as a single quadratic function which dips at dawn and dusk, can eliminate the dawn and dusk choruses (Fig. 7b).

Trends in the Discrimination Index

We now consider trends in DI (Figs 7 and 8). Modest increases in DI can indeed occur if pairing propensity changes through the day, so this is a strategy that females might be predicted to follow. Variation in pairing propensity by a large factor may or may not be superior to less dramatic variation. Looking across and down rows in Fig. 8 it is apparent that the trends are not always smooth; reversals and sudden drops in DI often occur. The broad pattern is the same whether a step function or cubic spline is used. These patterns generated by formal modelling are not always readily explained by verbal argument. Nevertheless a pattern does emerge of when it is best for a female to reduce her pairing propensity.
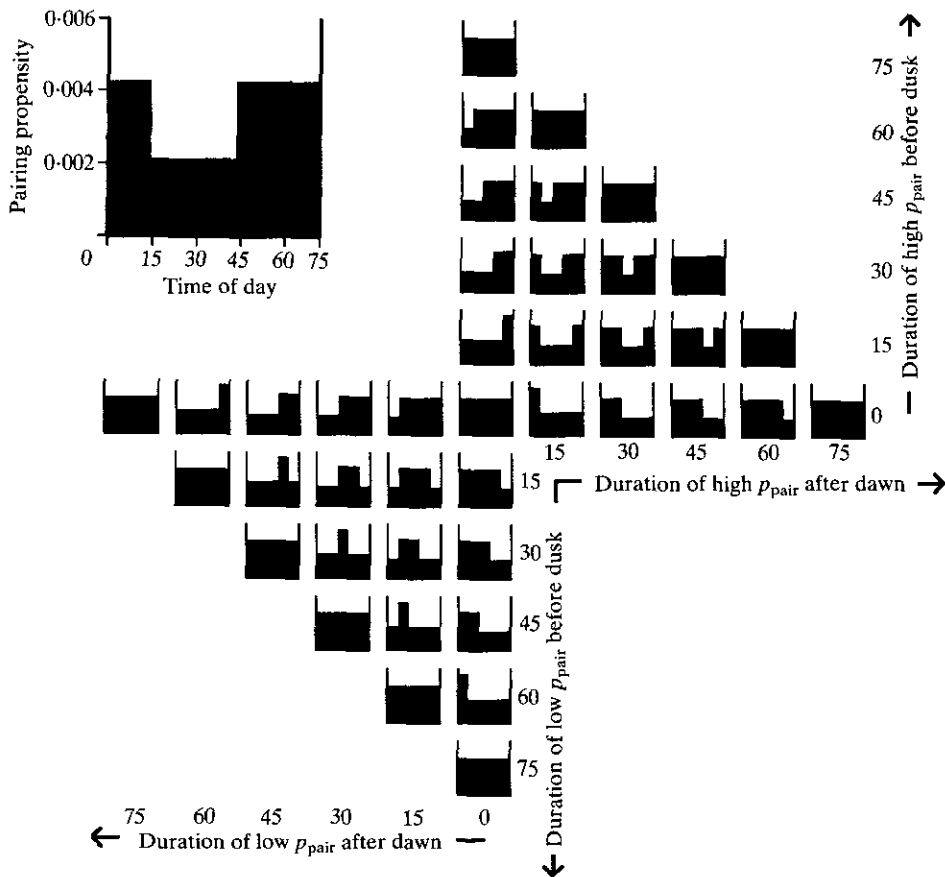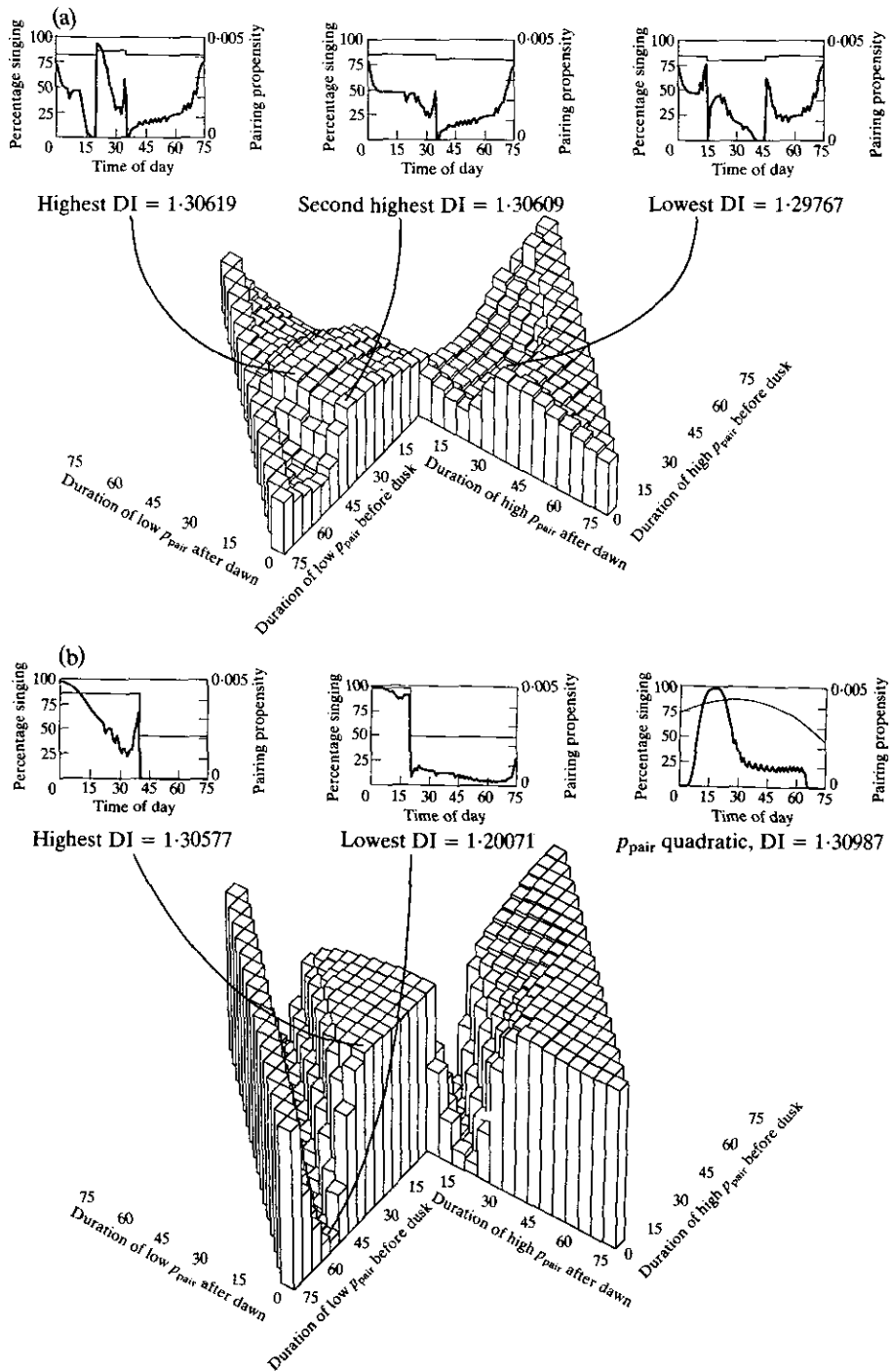
Figure 6. How the circadian variation of pairing propensity (p_{pair}) in Figs 7 and 8 is altered, except that here blocks of high and low p_{pair} vary by 15 intervals rather than 5. As in Fig. 7b, p_{pair} varies by a factor of 2 through the day; absolute values of p_{pair} differ between entries since p_{pair} is adjusted to ensure 10% daily pairing success. The baseline model of constant p_{pair} is shown at the start or end of each row and routines in which p_{pair} changes only once appear twice.

In our baseline model there are strong peaks of singing at dawn and dusk. A constant pairing propensity gives DI = 1·30288. Figure 7 shows the effect of systematically varying pairing propensity as described. Of the cases considered the highest DI is achieved by varying pairing propensity by a factor of 0·95 (Fig. 7a) rather than 0·5 (Fig. 7b), and involves a reduction in pairing propensity at dawn and dusk. Calculations were repeated using a cubic function to smooth out the change between blocks; again the highest DI is obtained by penalizing dawn and dusk. We also modelled pairing propensity as following a quadratic function over the day. Quadratics taking maximum values and those taking minimum values were considered, and the effect of the position of the extremum systematically

investigated. Figure 7b (top right) shows the quadratic pairing propensity with the highest overall DI. This quadratic again reduces pairing propensity at dawn and dusk, and peaks at approximately the same position as the best step-function pairing propensity. The DI for the best quadratic pairing propensity (1·30987) is greater than that for the best step function (1·30619), but neither is much greater than the DI for a constant pairing propensity (1·30288).

In the model with constant pairing propensities, we saw earlier that by altering various parameters it is possible to generate routines with a dusk chorus but silence at dawn, or with a dawn chorus but silence at dusk. In these cases also DI is increased if pairing propensity is decreased when the chorus would otherwise occur (Fig. 8).

Figure 7. The Discrimination Index (DI) as a function of circadian variation in pairing propensity. Column heights indicate DI as pairing propensity (p_{pair}) is varied in blocks of five time intervals through the day (see Fig. 6 for how these blocks are varied). When p_{pair} is constant the routine is the baseline and DI = 1·30288. (a) p_{pair} varies by a factor of 0·95; (b) p_{pair} varies by a factor of 0·5. Some very low DIs in (b) necessitate that the vertical scales of (a) and (b) differ. The routines (of intermediate-quality birds) generated by particular changes in p_{pair} are shown above (p_{pair} is also indicated). Routines are less smooth than in earlier figures because energy reserves were modelled here, as in all calculations of DI, with a coarser grid.
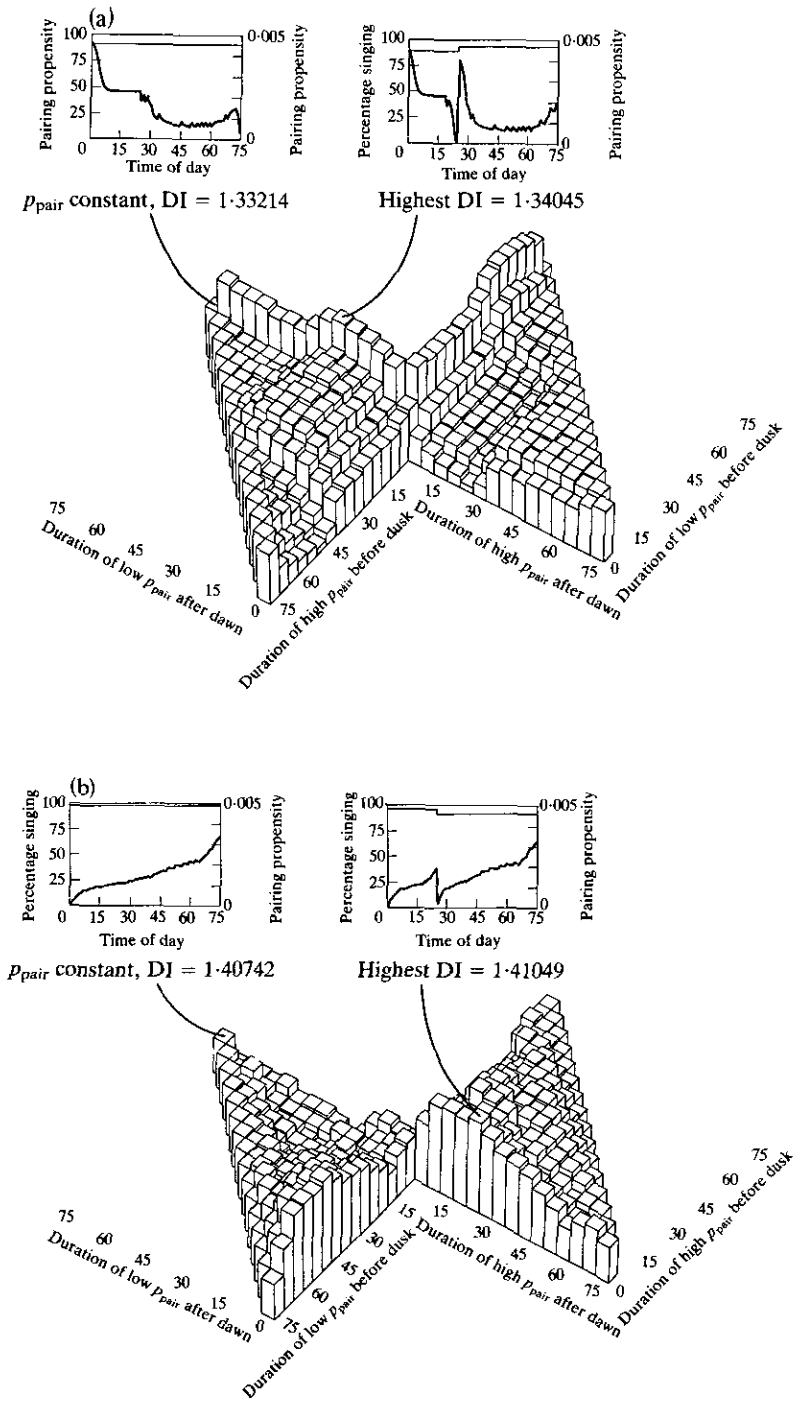
Figure 8. The Discrimination Index (DI) as a function of circadian variation in pairing propensity. Layout similar to Fig. 7a; p_{pair} is altered by a factor of 0·95 for differing periods through the day. Other parameters are chosen so that, when p_{pair} is constant, in (a) singing generally declines through the day (parameters as in line ● of Fig. 3), and in (b) singing increases through the day ($S_1 = S_2 = 0$, $e = 96$, $p_{food} = 0·2$, $q_{temp} = 0·9$). The highest DI occurs when the otherwise most popular time to sing is made less rewarding.

Stepwise changes in pairing propensity that produce the two highest DIs in Fig. 7a generate rather different routines. Both are very different to that generated by the best quadratic. Conversely the changes in pairing propensity producing the highest and lowest DIs in Fig. 7a nevertheless generate rather similar routines.

Female Memory

So far a male's probability of pairing during a time interval has not depended on how much he has sung previously. However, two factors favour female choice rules that depend on memory of past song. Because memory integrates song output over a series of time steps, the female is able to ensure that she does not pair with a male that sings for a small proportion of the day. A second reason is that with memory it is possible to distinguish a male that sings every second step from a male that can sing for half the day continuously. Because of the mass-dependent costs of fat accumulation, the second performance requires a higher daily energy intake and therefore should be considered more impressive. Even if memory were not advantageous in discriminating between males, a model of memory would still be of interest because it also describes the situation, perhaps more common in slow-moving amphibia and invertebrates, of the female requiring a long burst of male song in order to locate him. We now show that allowing females to remember past song can dramatically increase the Discrimination Index.

Methods

Our models rely on a state variable M which can take values between 0 and a maximum value, M_{max}. When a male sings M increases; when he is silent M decreases. We use two alternative rules to update the value of M.

(1) The continuous-run rule: if the male sings M increases by 1 unless M is at the maximum value, in which case it remains at M_{max}. M is set to 0 if the male does not sing. M therefore counts the length of a run of continuous song up to a maximum, M_{max}. (2) The linear-operator rule: these rules are widespread in learning models of foraging (McNamara & Houston 1985; Kacelnik et al. 1987) and have certain optimality properties (McNamara & Houston 1987). The linear operator rule depends

on a memory factor α which is a chosen constant lying between 0 and 1. In any time interval the previous M is updated to a new M' by the formula

$$M' = \alpha M + (1 - \alpha)M_{max}\varepsilon$$

where $\varepsilon = 1$ if the male sings and $\varepsilon = 0$ otherwise. M is thus a moving average of singing frequency, with song further in the past receiving exponentially less emphasis. The higher the value of α, the greater the importance of past song. Continuous singing results in M tending towards its maximum value M_{max}. For technical reasons explained in the Appendix M is also subject to a certain amount of noise in our model.

Whichever rule is used to update M, we also need to specify how the value of M affects the female pairing propensity. One simple possibility is that pairing propensity is proportional to M. We can equally well increase pairing propensity by a factor proportional to some power of M, or even use a step function such that pairing propensity is 0 unless M takes its maximum value M_{max}.

We always assume that a bird cannot pair during the night. Most results presented are based on the assumption that females take note of male song during the night. When this is so, a male may sing during the night to build up M and increase his chances of being chosen after dawn. Some routines in which females ignore male song at night, or equivalently male song is forbidden at night, are also presented.

The Discrimination Index

DI has a very clear-cut dependence on the length of female memory and on the relationship between memory and pairing propensity. Most importantly, note that the increases in DI far exceed those that were possible by allowing pairing propensity to depend only on time of day. DI for constant pairing propensity is 1·30288. Allowing time of day variation can increase DI to 1·30987 (Fig. 7b). Allowing memory (but not time-of-day dependence) typically increases DI to 1·4 or higher (Tables IV and V).

The continuous-run rule. First, the higher the value of M_{max} (i.e. the longer the memory), the higher is DI (Table IV). Second, making pairing propensity increase with, for example, M^2 is better than using lower powers of M, but higher powers are even better; and generally it is best of all if females pair only if the maximum value of M is

Table IV. Trends in the DI for the continuous-run memory model

	M_{max} = Maximum memory (time intervals)				
	1	2	4	8	16
Square root	1·303	1·323	1·337	1·360	1·405
Square	1·303	1·338	1·353	1·400	1·471
Step function	1·303	1·337	1·360	1·417	1·497

The length of maximum memory M_{max} increases across the table. The three rows differ in the dependence of pairing propensity p_{pair} on M. DI is highest when memory is long and when pairing may occur only if M is at its maximum value M_{max}.

Table V. Trends in DI for the linear-operator memory model

	α = Memory factor				
	0	0·2	0·5	0·8	0·95
Square root	1·303	1·309	1·321	1·357	1·424
Square	1·303	1·318	1·342	1·410	1·594
Step function	1·303	1·341	1·371	1·464	1·914

See legend to Table IV. Again length of memory increases across the table and DI increases to the bottom right.

attained (Table IV). In short, the harder the task that the female demands, the more the frequency of high-quality males attaining it exceeds that of low-quality males.

The linear-operator rule. We increase the length of memory by increasing α while keeping M_{max} contant. DI consistently increases as α increases and is again higher if the female pairs only when the maximum value of M is attained (Table V). Thus, as with the continuous-run rule, the harder the task a female sets males, the greater the probability that the male she pairs with is of high quality.

Comparison of the two rules. It is difficult to compare meaningfully the performance of the two types of rule since either can be improved by altering its parameters. To do so we specify that females pair only when M is at its maximum value M_{max}. We then introduce a source of noise into the continuous-run rule so that both rules have noise. For each rule the time taken for continuous song to raise M from 0 to M_{max} is then a random variable.

We set parameter values so that the two random variables arising from the two rules have the same mean and variance.

It turns out that the continuous-run rule has a higher DI than the linear-operator rule. Because the continuous-run rule is less forgiving of the occasional silence, it sets males a tougher challenge. However, we suspect that females in nature would not be so unforgiving. If the female by mistake misses a portion of a male's song, the continuous-run rule will lose her high-quality males that the linear-operator rule would accept.

*Resulting routines*

We present results for the linear-operator rule, but the routines generated by the continuous-run rule are qualitatively the same.

When there is a constant pairing propensity over the daytime and no memory, routines have no period of complete silence. Once memory is introduced there can be extended periods of no song as well as strong peaks (Fig. 9).
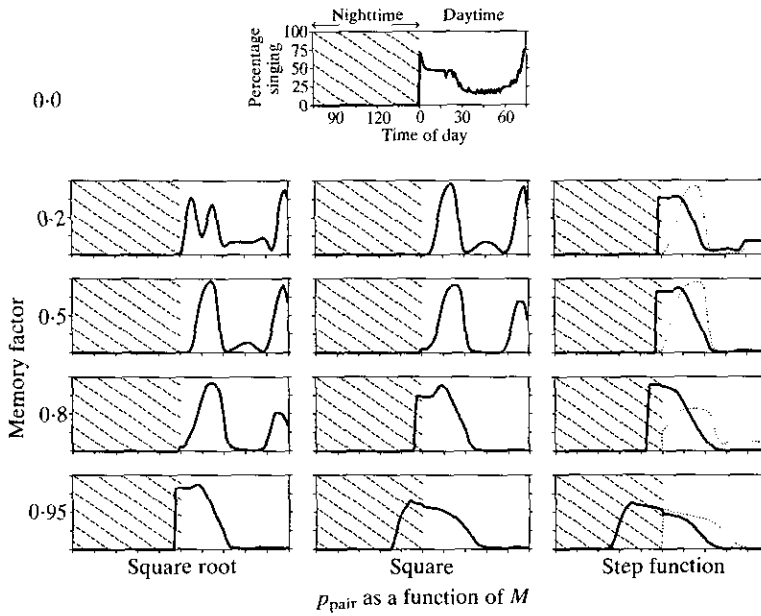
Figure 9. Dusk-to-dusk singing routines generated by the linear-operator model of memory. The top figure is the routine generated when there is no memory. Length of memory (α) increases down the table, whilst to the right pairing propensity increases more steeply with M. Solid lines show routines when singing (but not pairing) is permitted overnight; see Table V for the corresponding DIs. In the step-function case only, dotted lines show routines when night song is not permitted.
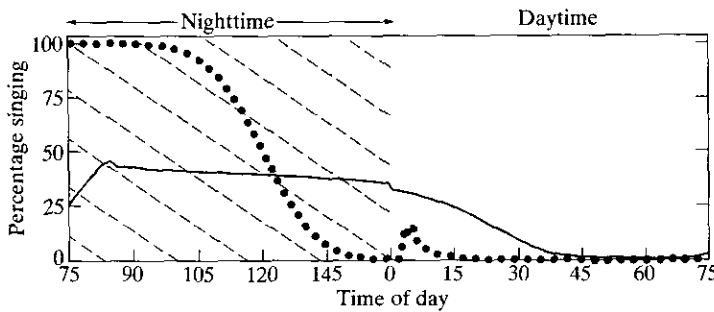

Figure 10. Dusk-to-dusk singing routines in which night singing dominates. The continuous line indicates an extreme routine generated by a very strong memory factor in the linear-operator model ($\alpha = 0.975$), pairing only permitted when $M = M_{max}$, a higher $M_{max} = 10$, and a reduced metabolic slope ($S_1 = 5 \times 10^{-4}$, $S_2 = 1.25 \times 10^{-6}$, $F_1 = 1 \times 10^{-3}$, $F_2 = 2.5 \times 10^{-6}$). The dotted line indicates baseline parameters with no memory, but pairing is permitted overnight.

The singing routines that emerge when memory is short are varied and are sensitive to parameters. Typically there are peaks of song at dawn and dusk, although there may be other peaks (Fig. 9). In particular there tends to be an extra peak of song in the morning. When male quality is reduced there tends to be a switch from singing at dawn to singing at dusk.

When females remember over longer periods, as consideration of DI says they ought, a more consistent pattern emerges. The more song a female demands before she will pair, the more the tendency for song to occur exclusively in a single block centred around dawn and stretching back into the night (Fig. 9). Before dawn males cannot pair but are singing to increase M and hence increase their chances of pairing at or just after dawn. With extreme levels of memory and low mass dependence we can generate a routine in which they sing throughout the night but pair only during the early part of the day (Fig. 10).
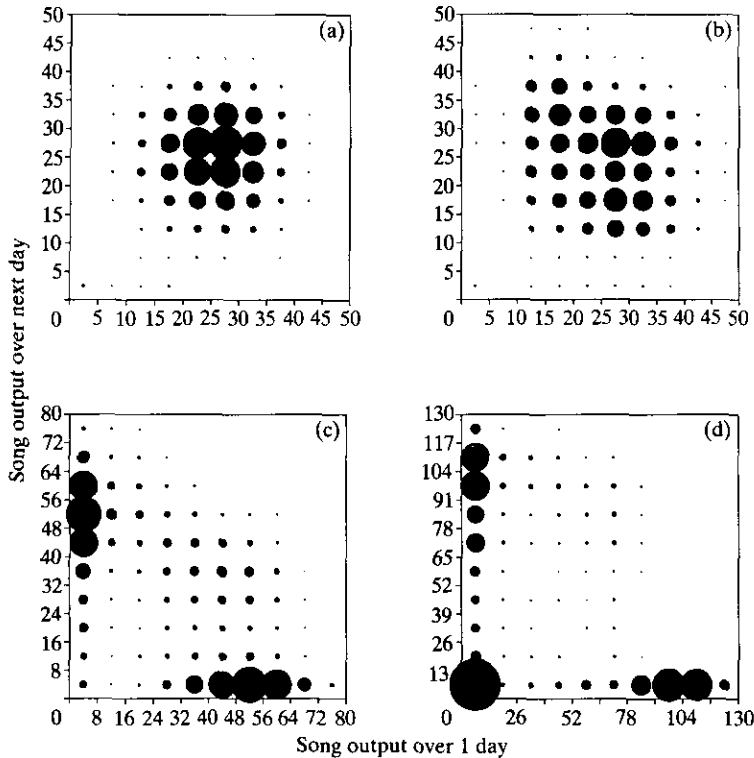
Figure 11. Day-to-day alternations in song output when memory is high: (a) baseline model (no memory), (b) memory factor $\alpha = 0.5$, pairing propensity (p_{pair}) increasing with M^2, (c) $\alpha = 0.95$, p_{pair} increasing with M^2, (d) $\alpha = 0.975$, p_{pair} a step function of M and reduced metabolic slope (parameters as in the continuous line of Fig. 10). Units on the axes are the number of time intervals spent singing per 24 h (24 h = 150 intervals). The area of a dot is proportional to how often each combination of song outputs occurred on consecutive days in 10 000 independent simulations. Some tendency for high output to lower output the following day is seen in (b); in (c) high and low output alternates from one day to the next; in (d) it usually takes 2 days of silence to rebuild reserves after a day of high output.

When song during the night is forbidden an increase in the length of memory again tends to eliminate the dusk chorus and produces a strong dawn chorus, although this chorus may peak after dawn (Fig. 9).

Whilst it is possible to construct a model with long memory in which the dusk chorus does occur to the exclusion of the dawn chorus, to do this we have simultaneously to forbid song at night, to increase the stochasticity of feeding, and dramatically to increase the mass dependence of feeding compared with that of song.

When females have long memories, males alternate their routines from day to day, husbanding resources one day so as to sing longer the next. This is not revealed by the displays of average song output shown so far; it is necessary, having found the optimum policies by dynamic programming, to simulate individual behaviour. These simulations

show that song output on successive days is uncorrelated when there is no memory (Fig. 11a). When memory is introduced song output on one day is negatively correlated with output on the following day, and positively correlated with output on the day after that (Fig. 11b,c). If mass dependence is decreased, longer periods of alternation can be achieved (Fig. 11d).

Female memory and time-of-day variation in pairing propensity

Prior to allowing females to remember male song output, we varied female pairing propensity with time of day and noted how dramatically it perturbed the optimal routines. The next obvious step is to combine these two approaches. Once again we divide the 75 steps of daylight into three blocks, the middle one of which differs in pairing

propensity. This time pairing propensity also depends on how long the male had been singing; we use a linear operator rule with a memory factor $\alpha = 0.8$ and pairing propensity non-zero only when the maximum value of M is attained.

As when no memory was involved, the increases in DI due to time-of-day variation in pairing propensity are modest and are greatest if pairing propensity is decreased when a chorus would otherwise occur. However, the routines are now much more robust to time-of-day variation in pairing propensity. Even when pairing propensity at dawn is reduced by a factor of 2, only if this reduction lasts a long time does silence occur at dawn and then only briefly, so that the morning peak remains. The discouragement of a true dawn chorus generates a subsidiary bout of song in the afternoon, but rather early for it to be considered a dusk chorus.

DISCUSSION

Females Should Make Males Work Hard

We have identified three ways for females to accentuate their discrimination in favour of high-quality males. They can lower their pairing propensity at all times, or be relatively less prone to pair at times when males otherwise find it optimal to sing, or demand that the male sings for long periods continuously. Also, DI is higher if song is metabolically more expensive. Intuitively speaking, the tougher the task demanded, the greater the ratio of high-quality to low-quality males that achieve it.

Time-dependent Variation in Pairing Propensity

Our model has established that optimal male routines are very sensitive to even slight time-of-day variation in pairing propensity (although increased mass dependence reduces this sensitivity somewhat).

Earlier discussions of the dawn chorus recognized several factors that may vary pairing propensity for a male. For instance, receptive females may accumulate overnight and thus be more abundant at dawn (Walker 1983; McNamara et al. 1987), and sound transmission (Henwood & Fabrick 1979) and the level of background noise (Brémond 1978; Gerhardt & Klump 1988) will vary through the

day. We have confirmed that, if these factors do determine how male pairing propensity varies, they will determine when song occurs, little hindered by the energy–time budgets that generated our baseline model (so long as females forget past song output).

The chance of a male pairing might also vary because females, despite hearing males, are reluctant to pair at certain times of day. We expressly tested one reason suggested for such time-of-day variation, that females would consequently be more likely to pair with high-quality males (Garson 1978; R. D. Montgomerie, loc. cit.). We showed that the potential increases in DI from such strategies are minute. It seems likely that the fitness benefits from these slight increases in DI will be outweighed by advantages to the female in pairing as soon as possible (discussed below) or in performing other tasks when she should be most responsive to song. (Mace (1987) criticized other aspects of Montgomerie's suggestion.)

As just mentioned, another reason for the female to be less willing to pair at certain times of day is if those are the best times for her to perform a conflicting activity. If the rituals of courtship interfere with feeding, we might envisage optimal female pairing routines arising for exactly the same reasons as do male singing routines. Pairing may be metabolically cheaper than singing and be performed less often, but that would not stop the optimal female routine from having the same form as our baseline: of greater female propensity to pair at dawn and dusk, and a dip in the afternoon when females are accumulating reserves to survive the night. Given this routine in female pairing propensity, male singing routines would adjust to mirror it.

Since optimal male routines are so sensitive to variation in the probability of pairing, and since such variation is to be expected, was it only coincidence that natural routines corresponded so strikingly to the male routine generated by our constant-pairing-propensity baseline model? We have now tentatively proposed an indirect explanation for the correspondence: a very similar model generates female routines, which in turn generate male routines. Female pairing propensity is harder to monitor than male song, but Mace (1989) has shown that relevant observations and experiments are possible. In some species we can simply monitor female attendance at communal display grounds (e.g. Snow 1962; Wiley 1991).

Memory-dependent Pairing

If females remember past performance, optimal male routines are much less sensitive to time-of-day variation in pairing propensity. DI is also little affected by such variation. Thus, when memory is used we need consider less carefully when females are free to pair (it may matter if they are not free to listen).

Memory affects DI markedly. The longer the female memory, the higher is DI, which leads us to ask what limits how long females should listen. This is important, because the optimal male routines when memory is long lack the dusk and midday choruses that occur when memory is short.

One factor limiting the length of female memory is that it depends on recognition of individual performances. This requirement also limits for which species memory models are applicable at all. Individual recognition of neighbours has been demonstrated in birds (Falls 1982; McGregor & Avery 1986). (Enabling females to monitor individual performance is another potential reason for inter-individual variation in bird song.) However, many phonotactic insects may rest their recognition merely on sound location (but see Lloyd 1981). If males of such species change position, or if satellite males accumulate round the singer (Perrill et al. 1978; Cade 1979), females have a restricted time in which they can monitor the song of a recognizable male.

Another constraint faces the female if monitoring males conflicts with other necessary activities, such as foraging or defending a territory. Although listening is less costly than singing, long continuous bouts might be an extra strain just as with singing. After some time fitness could be increased more by breaking off listening to perform other tasks than by checking that the male can sing longer.

Females that demand a harder task from males will have to wait extra days until some male passes the performance criterion. (When calculating DI we adjusted pairing propensity to maintain a constant pairing rate. In the wild females should never deliberately ignore a male achieving their performance criterion, so the probability that such males are paired depends on extrinsic factors such as whether females hear them.) Delays in breeding often have costs, for instance a reduced chance of a second brood or a decreased food supply (Daan et al. 1990). However, the most important cost restricting how long females listen before pairing is probably female competition for a limited supply of

males. We consider such intra-sexual interactions in the next section.

More Complex Models

Our model has several limitations that point to further avenues of research. We are not able to predict precisely what female decision rules will evolve, and nor therefore the male routines, because we have not sought an evolutionarily stable strategy (ESS). Further limitations are that when calculating DI we have assumed a stable bimodal distribution of male quality; we have been able only to guess what female strategies are optimum when female choice entails some cost; and we have ignored intra-sexual competition. To overcome these limitations would require a much more complex model.

Although this section concerns how our original model could be expanded to be more realistic, we stress that simplified models are worthwhile. The processes illuminated by our model would also occur in the more complex models but, confounded by other processes, would be less readily recognized.

Stability

In our model a male strategy's success depends on which strategy females use, and a female strategy's success depends on which strategy males use. We always find a male strategy that is optimal for a given female strategy, so if we had found a female strategy whose DI could not be improved, we might erroneously believe the pair of strategies to be evolutionarily stable.

But consider our result that lowered pairing propensity increases DI. In a large population of females who have chosen low pairing propensities a mutant female with a higher pairing propensity is equally likely to obtain a high-quality mate, since males will not adjust their strategy to the rare cheat. Thus, a low pairing propensity is not evolutionarily stable, and the value of this parameter will be set by factors independent of DI. (In general we expect advantages in pairing early to make females always keen to pair whenever they hear a male performance that passes their criterion.)

Although it seems plausible that using a long memory is an ESS, cheating is also to be expected with time-of-day variation in pairing propensity. In this case it is not clear that there exists a pair of

strategies in which the female strategy is optimal given the male strategy, as well as the male strategy optimal given the female strategy; quite possibly the ESS is mixed.

Relating DI to female fitness

To understand the impact of costs of choice on female behaviour we need to relate discrimination ability to female fitness. A first step is to quantify how paternal quality affects number and quality of offspring fledged. Quality need not be inherited for strategic handicaps to evolve (Grafen 1990a). Second, we need to specify how quality varies amongst males.

In reality changes in the environment stochastically shift the distribution of quality each generation. In a year without low-quality males, choosiness may be less advantageous. (However, in our restricted manipulations of male quality we did find that rules good at distinguishing high and intermediate quality also discriminated well intermediate and low quality.) In this more complex scenario, an optimum female strategy might consist of an initial phase in which females were less concerned to pair than to estimate the distribution of male quality that year.

Intra-sexual competition

So far we have assumed that each male and female has no direct competitors or that there is an infinite surplus of potential mates. In our Utopia females need not worry that a less choosey neighbour is about to snap up a high-quality male, because the availability of high-quality males would be unaffected.

In reality the local supply of high-quality males will be limited. Females that wait too long to pair will find only inferior males left; they may even run out of males altogether, or at least of males with territories. The optimum strategy will be an ESS-type balance between making up one's mind before competing females, and being more certain of pairing with a high-quality male (Collins & McNamara, in press). When local populations are small, stochasticity will play a role in determining the availability of males, which is another reason why females might concentrate initially on estimating numbers and quality of males in the neighbourhood. We have been modelling a constant-threshold criterion, but in these circumstances best-of-*n*

decision rules or sequential searches with changing thresholds would have advantages (Real 1990).

Female strategy should depend also on the number of female competitors for mates. We do not know if or how females can estimate this, but a male only has to listen to estimate numbers, qualities and strategies of his competitors. Males may wait to avoid their song being obscured by neighbours' song (e.g. Gochfeld 1978; Cade 1979); in other cases synchrony may be attractive to females or dilute predation risk (Cade 1981; Ryan et al. 1981; Walker 1983). We expect the optimum strategy often to take account of the male's own quality and of his estimate of competing males' qualities and strategies. (On a shorter time-scale, individual nightingales, *Luscinia megarhynchos*, avoid overlapping some individuals but consistently overlap others; other individuals always overlap or always avoid overlapping: Hultsch & Todt 1982).

Even if strategies are not so sophisticated as to respond to individual performances of neighbours, a longer-term evolutionary response may still affect the times of day when birds sing. Thus, Houston & McNamara (1987) retained infinite populations with no quality variation, but they increased or decreased female pairing propensity with the proportion of males singing at each time of day. They showed that, if males avoid singing at times of day when others are singing, optimal routines are very unstable (any ESS is probably mixed), whereas if it is advantageous to sing synchronously, choruses are magnified. A similar magnification of a chorus should occur if male song is directed towards males, and males listen most when they are singing.

Finding solutions in a complex model

Houston & McNamara's (1987) model required finding an ESS for a stochastic dynamic game, one of the most complicated games for which an ESS has been found. Yet this simplified the male–male interactions likely in nature and avoided altogether the frequency-dependent female–male and female–female interactions outlined earlier. Dynamic programming is not a realistic method to find optima in these more complex models, because the computational load increases disproportionately with each new state variable (we would need to introduce new state variables for each player in the game). Genetic algorithms are a more promising technique (Sumida et al. 1990). Besides finding near-optimal routines, this technique indicates how

directly and how quickly the optimum strategy will evolve.

The Handicap Principle

As noted earlier, song acts via the handicap principle to be an honest signal of male quality. Grafen (1990a, b) has shown that the handicap principle will generate an ESS of honest signalling; this suggests that a more complete version of our model would generate such an ESS.

We emphasize that song is used as an honest signal only because it is expensive (in that it risks starvation). We found that the more metabolically expensive song is, the more reliable the signal. In other instances singing is costly in attracting predators (Burk 1988). If males differ in ability to escape from predators (perhaps because of size or wounds), females may use song as an honest signal of this other aspect of male quality. Males will try to cheat by generating song more efficiently or safely, but if they discovered a type of song without risk to their viability, males could all sing equally and females should take no note of that song as an indication of quality. Vigour of the display should also be influenced by the handicap principle, so long as females cannot be misled as to how much energy a male is consuming.

The handicap principle can operate outside the context of sexual selection (Grafen 1990b; Zahavi 1991). For instance, suppose that song served to warn predators that the animal was vigilant and thus not worth attacking (Hasson 1991). The skylark, *Alauda arvensis*, can adapt its song flight for this purpose (ap Rhisart 1989), and we can readily adapt our model so that the only incentive for song is decreased predation. Again high-quality males can afford to sing more often, so that their display of vigilance also becomes an honest signal of quality, whether or not the predator uses this information. (It is not obvious whether the fact that an expensive signal is already 'paid for' by warding off predators should, to a mate, make it a more or a less reliable signal of quality. Thanks to having a formal model, we are able to report that a dual function can increase DI.)

Extended Applications

In this section we extend the application of our model both by reinterpreting to what the parameters refer and by arguing that changing certain features of the model hardly affects the results. However, we stress that there is no universal model describing the costs and benefits of song. We would rather that fieldworkers did not use our results to explain their animal's behaviour, but that they use our principles to construct their own models.

Other functions of song

Although our model considers only a single pairing, we would expect similar routines if a male had further low probabilities of pairing again. We have not considered when pairing is so frequent that depletion of energy levels in an effort to pair once would significantly delay pairing again.

It makes no difference to the working of the model whether by 'pairing' we mean mating or a preliminary stage of bonding, especially as results are robust to alterations in the terminal reward. As long as song increases expected reproductive success, its purpose need not even directly concern females. For instance, our model might equally well represent males signalling quality to other males in order to win a territory.

As mentioned above, it is straightforward to adapt our model to include predation. The probability of predation could depend on activity, mass, whether it is day or night, and time of day. One possibility is that singing attracts predators and that fat animals escape less easily (Blem 1975; Witter & Cuthill, in press); this should reduce the dusk chorus.

Alternatively singing may deter predators, as discussed above. We adapted our model so that the incentive for singing was no longer mate attraction but just that it decreased predation; routines are very similar to our baseline case. Whereas before males sang in order to achieve a rare reward, here they sing to avoid a rare penalty. The latter may have greater similarities to territory defence.

We predict similar routines, therefore, whether the function of song is attracting a single mate, attracting occasional extra-pair copulations, winning a territory, or defending a territory. Yet observed routines may change considerably during the breeding season when birds redirect song to different listeners (e.g. Verner 1965; Grüll 1981). This suggests that special factors are important, such as time-of-day variation in the attention of listeners.

We need not necessarily alter the framework of the model to examine routines in different modalities of communication, such as dances

(Endler 1987), light emission (Dreisig 1971), pheromone release (Landolt & Heath 1987), or social grooming. This is true as long as such signals consume energy or interfere with feeding. The model may not be directly applicable when animals alternate feeding sessions with non-feeding periods necessary for digestion but which might also be used for advertisement. The model might further be applied to non-communicating activities that conflict with feeding, but that need not be performed at specific times or in response to extraneous stimuli, for instance play activity, preening or nest construction.

Night singers

For birds such as some owls and nightjars, which feed and sing at night but are inactive in the day, the only alterations required to the model are renaming day and night. Other night singers remain stationary at night (Martin 1990), not feeding but possibly attracting mates, especially if female migrants arrive at night. Figures 9 and 10 show that, with memory, there is no need to invoke nighttime pairing to explain night singing that is continuous with the dawn chorus (many dawn choruses start when it is still pitch black to us: Åström 1976; Barclay et al. 1985 showed a routine with song starting in the middle of the night). However, we can modify our model to allow pairing at night. In the version with no memory song output increases immediately after dusk and then declines to silence during the night; another chorus may occur around dawn (Fig. 10). This resembles routines of certain other night singers (Toivari & Lindqvist 1962; Sorjonen 1977).

Other taxa

Our results for birds should apply to calling mammals, although in four primate species from Sumatra only one species exhibited a baseline-like routine, and two other species (both gibbons) peaked in late morning (Mackinnon 1974). East & Hofer (1991) gave examples of mammals that do peak at either dawn or dusk.

The other groups for which singing routines are best known are Orthoptera, frogs and cicadas, reviewed by Walker (1983). Dawn and dusk choruses are often a feature of their routines.

We have already mentioned that such phonotactic animals may act as though they use a memory (see also Hedrick 1986). However, one problem in applying an unmodified version of our model to Orthoptera and cicadas is that they could potentially feed at any time of the day or night.

The weather

We are also wary of applying our model to non-aquatic ectotherms because temperature is likely to be a major influence on when singing is optimal or even possible. A regular temperature fall is an obvious explanation why their dusk choruses often do not continue through the night. When low temperatures prevent ectotherm activity, energy losses will be minimal compared with nightly energy expenditure in diurnal endotherms. In arid environments extremely high midday temperatures limit activity in ectotherm and endotherm alike, generating the equivalent of another night.

Temperature changes also disrupt our predictions for those birds whose main prey is mobile ectotherms (Avery & Krebs 1984). McNamara et al. (1987) altered their model to include time-of-day variation in foraging success. They noted that routines do not always change as we would intuitively expect.

Another aspect of the weather is the threat of unpredictable prolonged interruptions to foraging. For instance many birds are inactive in the rain, and rainstorms are a frequent but fairly unpredictable occurrence in tropical rain forest. Preliminary calculations indicate that the threat of even weekly hour-long interruptions can markedly alter the routine, for instance causing the dusk chorus to peak earlier in the afternoon.

Testing the Model

Modelling can show some explanations to be logically flawed, but its main role in testing hypotheses is to generate testable predictions. The evidence advanced so far for the biological significance of our baseline routine is mainly its agreement with 'typical' temperate passerine song ouput. It would be more convincing to show agreement with routines for other latitudes, separate species, separate populations, or, best of all, for individuals' song output. Gathering such

Table VI. Parameters and their baseline values

Symbol	Meaning	Baseline value
e	Energy content of food patch	32
p_{food}	Probability foraging bird finds a food patch	0·6
S_0	Determine mean metabolic	12
S_1	expenditure while singing and	1×10^{-3}
S_2	how this mean depends on reserves	$2\cdot5 \times 10^{-6}$
η_s	Determine variability of	6·4
q_s	metabolic expenditure while singing	0·5
F_0	Determine mean metabolic	8
F_1	expenditure while foraging and	2×10^{-3}
F_2	how this mean depends on reserves	5×10^{-6}
η_f	Determine variability of	6·4
q_f	metabolic expenditure while foraging	0·5
R_{cold}	Resting mean metabolic rate on a cold night	3·6
R_{normal}	Resting mean metabolic rate on a normal night and during the day	2·8
R_{warm}	Resting mean metabolic rate on a warm night	2·6
q_{temp}	Probability that a night is normal	0·8
η_r	Determine variance in	0
q_r	nighttime resting metabolic expenditure	1
p_{pair}	Pairing propensity	4×10^{-3}

data requires long hours in the field, so most published data concern single days (e.g. Snow 1962) or repeated observations on just the dawn chorus (e.g. Garson & Hunter 1979).

Even when the singing routine of a species is well known, all we can usually do with these data is to argue that our model can generate similar routines. This argument is weak since we make no claim that other factors are not superimposed on our model; observed routines that our model cannot readily fit (e.g. the midday peak of the manakin *Manacus manacus*; Snow 1962) do not falsify the hypothesis. Another weakness is that we are free to manipulate poorly known parameters until the model fits. Three further approaches would provide greater stringency: (1) measuring parameters more accurately for a model tailored to a particular species; in the case of mass dependence, for instance, this would be difficult, especially if the effect concerned rare incidents of predation; (2) a comparative approach; for example, the metabolic slope on singing is presumably higher in species with an aerial display; (3) experimental manipulations; for example, an artificial perch would reduce metabolic slope on singing if birds used it in preference to an aerial display.

The Results section gives our predictions for how each parameter influences the routines. The model also predicts whether one day's exertions will affect activity the following day, the distribution of song-bout length, when pairings occur, and the relationship between weight and singing activity. But beware that the predictions made in the Results section envisage that the policy has had time to adjust optimally. Predictions may differ when short-term experimental manipulations (e.g. Cuthill & Macdonald 1990) affect only the routine and not the policy.

Besides generating predictions, modelling has further served to identify important gaps in our knowledge. A better understanding of mass dependence and stochasticity is evidently crucial. We know very little about how females apportion their time between feeding and mate seeking (Mace 1989), whether females listen to song before dawn, and the time-scales over which females assess performance (Hedrick 1986; Sullivan 1990). Ornithologists should also more thoroughly study when birds sing, total song output, and song bout-length (and in particular assess the fitness consequences), rather than solely examining song structure and repertoire size.

APPENDIX

Food and metabolic parameters and their baseline values are summarized in Table VI.

Model Specification
Time
We divide each 24-h period into 150 time intervals. Time 0 is dawn, time 75 dusk, and time 150 is time 0 on the next day.

Reserves

Energy reserves take non-negative integer values. Let the bird have reserves $i \geq 1$ at time t. Suppose he finds food of energy content E and uses metabolic energy D between time t and $t+1$. Define $x = i + E - D$. Then reserves at time $t+1$ are

$$\text{maximum } \{0, [x]\} \text{ with probability } 1 + [x] - x$$
and
$$\text{maximum } \{0, [x] + 1\} \text{ with probability } x - [x],$$

where $[x]$ denotes the integer part of x.

If reserves reach zero the bird dies of starvation.

Food found

As above, let E denote the energy content of the food found during a time interval. $E = 0$ if the bird forages during the night, rests or sings. If the bird forages during the day

$$E = e \text{ with probability } p_{food}$$
and
$$E = 0 \text{ with probability } 1 - p_{food}.$$

Metabolic expenditure while singing

A bird that has reserves i at time t and sings between times t and $t+1$ expends

$$D = d_s(i) + B_s$$

during this time interval, where

$$d_s(i) = S_0 + S_1 i + S_2 i^2$$

and

$$B_s = -\eta_s \text{ with probability } \tfrac{1}{2}(1 - q_s)$$
$$B_s = 0 \text{ with probability } q_s$$
$$B_s = \eta_s \text{ with probability } \tfrac{1}{2}(1 - q_s).$$

Metabolic expenditure while foraging

A bird that has reserves i at time t and forages between times t and $t+1$ expends $D = d_f(i) + B_f$ where $d_f(i) = F_0 + F_1 i + F_2 i^2$ and $B_f = -\eta_f$, 0 or η_f with probabilities $\tfrac{1}{2}(1 - q_f)$, q_f and $\tfrac{1}{2}(1 - q_f)$, respectively.

Resting metabolics

During the day the expenditure while resting is $D = R_{normal} + B_r$ per time interval, independently of reserves, but birds never chose this option. At night expenditure is $D = d_{rn} + B_r$. Nights are cold, normal and warm with probabilities $\tfrac{1}{2}(1 - q_{temp})$, q_{temp} and $\tfrac{1}{2}(1 - q_{temp})$, respectively. When the night is cold $d_{rn} = R_{cold}$, when normal $d_{rn} = R_{normal}$ and when warm $d_{rn} = R_{warm}$. $B_r = -\eta_r$, 0 or $+\eta_r$ with probabilities $\tfrac{1}{2}(1 - q_r)$, q_r and $\tfrac{1}{2}(1 - q_r)$, respectively.

Memory

We describe in the text how M is updated using the continuous-run rule. When M is updated using the linear-operator rule, formula (1) gives an M' which is non-integer. We therefore set the new M to be

$$[M'] \text{ with probability } 1 + [M'] - M'$$
and
$$[M'] + 1 \text{ with probability } M' - [M'],$$

where $[M']$ denotes the integer part of M'. Thus the change in M is stochastic.

For the linear-operator rule we normally set $M_{max} = 5$.

Pairing propensity

Let p_{pair} be the probability a male pairs in one time interval. Then $p_{pair} = 0$ if the bird rests or forages. Also $p_{pair} = 0$ during the night. When there is no memory p_{pair} for a singing bird is a function of time of day and is independent of previous song. When there is memory p_{pair} is a function of M and possibly of time of day.

Reward structure

The window over which a male can pair terminates at the end of each time interval with a constant probability. On termination a paired male receives a reward of 2, an unpaired male receives 1 and a dead male receives 0. The optimality criterion is maximization of expected reward.

The optimal policy could be found by various means. We employ dynamic programming over a finite time horizon, working backwards until policies and the expected terminal reward converge as time to go becomes large. Routines are found by following birds forward in time until there is convergence to a limit in the probability that a live and unpaired bird becomes paired within 24 h. In working forward we assume that night temperatures are normal and that the pairing window does not end.

DIs are calculated using a coarser reserve grid than the one described above. Successive grid points for this coarse grid are 4 of the above units apart.

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