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Annual routines of non-migratory birds: optimal moult strategies

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In a periodically changing environment it is important for animals to properly time the major events of their life in order to maximise their lifetime fitness. For a non-migratory bird the timing of breeding and moult are thought to be the most crucial. We develop a state-dependent optimal annual routine model that incorporates explicit density dependence in the food supply. In the model the birds' decisions depend on the time of year, their energy reserves, breeding status, experience, and the quality of two types of feathers (outer and inner primaries). Our model predicts that, under a seasonal environment, feathers with large effects on flight ability, higher abrasion rate and lower energetic cost of moult should be moulted closer to the winter (i.e. later) than those with the opposite attributes. Therefore, we argue that the sequence of moult may be an adaptive response to the problem of optimal timing of moult of differing feathers within the same feather tract. The model also predicts that environmental seasonality greatly affects optimal annual routines. Under high seasonality birds breed first then immediately moult, whereas under low seasonality an alternation occurs between breeding and moulting some of the feathers in one year and having a complete moult but no breeding in the other year. Increasing food abundance has a similar effect.

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In an environment that changes periodically over the year the timing of the major events in an organism's life can have large effects on the organism's survival and reproduction, and we would expect natural selection to shape the order and timing of these behaviours to maximise fitness (McNamara et al. 1998, Houston and McNamara 1999). Proper timing is important for a number of reasons. First, the benefits from these events can vary significantly over the year (e.g. the survival and subsequent reproduction of young may depend on the time in the season at which they are born, Lack 1968, Guinness et al. 1978, Daan et al. 1989, Green and

Rothstein 1993, Verboven and Visser 1998, Székely and Cuthill 1999, Cote and Festa-Bianchet 2001). Second, performing an action at a given time may significantly influence the animal's future state which in turn may influence its available actions in the future. For example, when an animal migrates, it changes both its location and its energy reserves. In turn these changes influence whether the animal can breed and if it breeds how successful the attempt may be. Third, the performance of one activity may exclude the performance of others (e.g. most species cannot breed during migration). In this latter case the optimal time to perform a given activity

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will not only depend on the best time for this action but also on whether there are other good times to perform the excluded activities (Foster 1975, Houston and McNamara 1999). A general technique for finding optimal annual routines is presented by Houston and McNamara (1999) and is used in the context of migration by McNamara et al. (1998), and used to investigate the effects of the background mortality rate on annual routines in McNamara et al. (2004). The technique can be employed to analyse a wide range of issues. In this paper we concentrate on the timing of reproduction and moult in non migratory species of bird. Although our detailed results are specific to this case the underlying tradeoffs are likely to occur in other contexts.

For a non-migratory bird the timing of breeding and moult are thought to be the most crucial (Immelmann 1971). Breeding is significant because of its obvious impact on the bird's reproductive success and because of its well documented costs in terms of energetic expenditure and survival (Gustafsson and Sutherland 1988, Nilsson and Svensson 1996). Moult (the process in which birds renew their plumage regularly) is important because it restores the state of the otherwise continuously deteriorating feathers. Reduced feather quality reduces flight ability and hence increases flight metabolism and may reduce a bird's ability to escape from predators. Consequently, moulting has advantages in terms of future performance. However, it also has immediate costs. During moult, flight performance may be severely affected (Haukioja 1971, Swaddle et al. 1996, Chai 1997, Swaddle and Witter 1997, Hedenström and Sunada 1999; but see Lind 2001), and regrowth of the feathers requires energy and protein (King 1980, Klaassen 1995, Murphy 1996).

The organisation of annual routines is basically the same for most non-migratory temperate zone birds; a breeding season is followed by a complete moult (post-nuptial moult) with relatively rare moult-breeding overlap (Ginn and Melville 1983, Jenni and Winkler 1994). The annual routines of the tropical species are much more variable. In addition to the most common post-nuptial moult there is also prenuptial moult (Brooke 1985), moulting while breeding (Craig 1983, Franklin et al. 1999), a complete moult surrounded by a biannual breeding season (Wilkinson 1983) or a complete moult following each of the two breeding periods (Miller 1961). Tropical birds also tend to have smaller clutches and live longer than temperate zone ones (Lack 1947, Ricklefs 1980, Murray Jr. 1985, Martin 1996, Stutchbury and Morton 2001). Considerable variability exists, furthermore, in the detailed structure of annual schedules of different populations and species both in the temperate zone and in the tropics. For instance, the start of both breeding and

moult, the number of broods, the length of a breeding attempt, and the length and intensity of moult can all vary among individuals, sexes, populations or species (Davis 1971, Stiles and Wolf 1974, Ginn and Melville 1983, Thompson 1988, Jenni and Winkler 1994, Franklin et al. 1999, Hemborg et al. 2001). It is, however, largely still unclear what ecological, evolutionary or life history factors are responsible for the evolution and maintenance of between species variability (Svensson and Hedenström 1999). Furthermore, even less is known about both the occurrence and the causes of individual variation of annual routines within a species (Hemborg 1998).

The sequence of primary moult within a feather tract (in which the main flight feathers on the wings are replaced) is much less variable than its timing, speed etc. Most species of birds follow the so called basic sequence of moult (or descendant primary moult) in which the innermost primaries are dropped first and then primaries are replaced in an outward direction (Jenni and Winkler 1994). Apart from a hypothesis which suggests that descendant replacement is the easiest way to reduce the effect of lift forces on a growing primary during flight (Noordhuis 1989), the reason for this pattern has not been considered.

Here we present a detailed model to improve our understanding of the timing of reproduction and the timing and sequence of moult in non-migratory birds. Using the approach of Houston and McNamara (1999) allows us to relax most of the restrictions imposed by previous modellers (Holmgren and Hedenström 1995). For instance, we allow flexibility in both the time of breeding and the number of broods (including the option not to breed at all), and we allow activity to influence the state of the feathers. Furthermore, we use explicit density dependence which makes it possible to more accurately investigate how factors such as the food supply influence annual schedules. We also include two different feather types in our model to give a more detailed account of moult. For instance, we can model aspects of the speed and sequence of moult.

Our aim is to investigate how individual characteristics (e.g. quality of feathers, breeding status and energy reserves) influence the annual routines of birds. Furthermore, by introducing different kinds of asymmetry between the two types of feathers we establish the factors influencing the sequence of moult. We also investigate the effects of environmental factors (seasonal variation, abundance of food and background mortality) on the organisation of annual routines (e.g. the timing and order of moult) in non-migratory birds. We place great emphasis on the comparison of highly seasonal, less seasonal and aseasonal environments in order to explain why annual routines are more variable in the tropics.

The model

As the electronic supplement contains the detailed description of the model here we only emphasise the main points.

We consider the behaviour of a female bird and all her female descendants over a period of many years. Each year is divided into $T = 52$ weeks, where week 0 is the middle of the winter. At the start of each week (i.e. at times $t = 0, 1, \dots, T - 1$), the bird has available four classes of behavioural actions relating to (i) moult of the outer primaries, (ii) moult of the inner primaries, (iii) foraging intensity, and (iv) reproductive behaviour. It simultaneously performs one action from each class. The performance of an action in one class does not constrain the action performed in another class. The action taken by the bird can depend on the time of the year and its state which is represented by five state variables: quality of its feathers (outer and inner primaries, ${}_oF$ and ${}_iF$), experience e , age of the brood a and energy reserves r . The action taken influences the bird's future state.

Feathers and moult

We have chosen to model the moult of a bird's primary feathers rather than other feather groups for two reasons. First, primary moult extends over virtually the entire moult period and is usually taken as a reference for the process of moult in the other feather tracts (Jenni and Winkler 1994). Hence, the moult of primaries is well studied and so the timing and sequence of primary moult is better known than those of other feather tracts. Second, primaries are considered to be the feathers that have the strongest effect on flight ability (Jenni and Winkler 1994).

Instead of constructing a detailed model of individual feathers, we clump the primaries into two groups, the inner and outer primaries. This enables us to make predictions about the sequence in which the primaries are moulted and the speed of moult (measured by the extent of the overlap between the moult of the two groups). In some members of at least five groups of birds (albatrosses, parrots, owls, kingfishers and falcons) a group of inner primaries is moulted separately from the outer primaries (Filardi and Rohwer 2001). Our model is able to make predictions about when this pattern of moult should occur.

Both feather quality variables (${}_oF$ and ${}_iF$) can vary between 0 (very poor condition) and 1 (newly moulted feathers). Computations are based on the assumption that feather wear is proportional to foraging intensity, but we later comment on the robustness of conclusions to this assumption. Decreasing feather quality decreases flight ability and so increases predation risk and energy expenditure.

Starting moult of feather type j results in an instantaneous change in the feathers' state at the beginning of the week to ${}_jF_t = -{}_jm_{\text{length}}$. The state of feathers then tends to increase stochastically until ${}_jF_t = -1$ when the bird will deterministically have completely new feathers at the start of the next week, i.e. ${}_jF_{t+1} = 1$. Since feathers are renewing gradually during moult we assume that the flight ability of a moulting bird increases as moult progresses. Moulting flight feathers, however, decreases the bird's energy reserves because of the energy used for the synthesis of new feathers (Lustick 1970, Lindström et al. 1993).

Energy intake

The exact amount of food available in week t , $g(t)$, depends on the environmental food supply and the competition between birds for this food. The environmental food supply, $G(t)$, varies sinusoidally over the year. Its yearly average is given by A_{food} while its maximal deviation from the average is denoted by ε . The food supply has a maximum ($A_{\text{food}} + \varepsilon$) at midsummer and a minimum ($A_{\text{food}} - \varepsilon$) at midwinter. We assume that A_{food} and ε are the same for all years. At the beginning of each week the bird adopts a foraging intensity, u ($0 \leq u \leq 1$), and forages with this intensity throughout that week. We assume that the gross energy intake is proportional to foraging intensity. Because it is reasonable to assume that newly fledged birds forage with lower efficiency than adults, we introduce the state variable experience, e . The newly fledged birds are all inexperienced ($e = 0$) and experience tends to increase after fledging until full maturation ($e = e_{\text{max}}$).

The bird's energy intake, γ , depends on its foraging intensity, the availability of food, and the bird's experience as follows

$$\gamma(u, e, t) = ug(t)\theta^{e_{\text{max}} - e} \quad (1)$$

where $\theta < 1$.

Reproduction

For simplicity, we assume uniparental care. A non-caring bird can either immediately start a new brood (hereafter labelled as 'start') or alternatively 'subsist'. If the bird starts a new brood, the bird's reserves are decreased by an amount of energy Δ_s .

If the bird has a brood younger than the maximum brood age (a_{max}) it can either continue to care for it and so retain the brood ('care') or desert it ('desert'). If a bird deserts, its brood dies and the bird will have no brood during the next week. If the parent bird dies between t and $t + 1$ or is unable to achieve a gross energetic intake γ_{brood} during this period then all brood members starve to death. In order to get gross intake γ_{brood} , the bird

must forage with intensity at least equal to $u_{crit}(e, t)$ where $\gamma(u_{crit}, e, t) = \gamma_{brood}$. Thus if $u_{crit}(e, t) > 1$ the bird is forced to desert the brood since brood members will starve even if the mother forages with maximum intensity, $u = 1$. If $u_{crit}(e, t) < 1$ and the parent bird forages with intensity u , where $u_{crit}(e, t) \leq u \leq 1$, then the nestlings survive and the parent bird receives a gross energy intake of $\gamma(u, e, t) - \gamma_{brood}$.

If the brood reaches the maximum brood age (a_{max}) the bird abandons the brood ('abandon') and the nestlings become independent. We assume that their reserves are $r = 0.5$ and their feathers are in top quality, ${}_jF = 1$, ($j = o, i$). A bird who deserts or abandons its brood during week t cannot start a new brood before week $t + 1$. For simplicity, and because we are mainly interested in moult, we do not optimise over brood size. Instead the number of female young at abandonment n_{brood} is a parameter of our model. Note, however, that the modelled birds still can control their reproductive effort per year by varying their number of breeding attempts.

Energy reserves

The bird's energy reserves, r , vary between $r = 0$ and the bird's maximal storage capacity $r = 1$. We do not consider stochasticity in the food supply and stochasticity in metabolic expenditure separately, but instead combine chance events into an overall stochasticity in the change in reserves over a week. First, we consider the cases where the bird does not have a brood. If the bird subsists and forages with intensity u during week t its reserves at the start of the next week $t + 1$ are then given by the random variable $r_{subsist}$, where

$$r_{subsist} = r + \gamma(u, e, t) - C_{subsist} + R \quad (2)$$

Here R is a random variable with zero mean. The distribution of this random variable is specified in the electronic supplement. $C_{subsist}$ is the energetic expenditure of a subsisting bird. This expenditure depends on the bird's reserves, its foraging intensity and the quality of its feathers. The effect of starting a new brood can be described in a similar way:

$$r_{start} = r + \gamma(u, e, t) - C_{subsist} - \Delta_S + R \quad (3)$$

Now suppose that the bird has a brood and continues to care for it. Then it must forage with intensity u , $u_{crit}(e, t) \leq u \leq 1$, in order to ensure the survival of its nestlings. Its reserves will then be

$$r_{care} = r + \gamma(u, e, t) - \gamma_{brood} - C_{subsist} + R \quad (4)$$

Sources of mortality

The bird can die because of starvation or predation. Starvation occurs when $r = 0$. We assume that predation risk is an accelerating function of foraging intensity (the higher the intensity, the less probable is the bird to detect an approaching predator), and body reserves (the more reserves it carries, the less likely it can escape from an attack; Witter and Cuthill 1993, Cuthill and Houston 1997). Predation risk decreases with flight efficiency $E(oF, iF)$; the more impaired the bird's flight is, the less likely it can escape from an attack (Hedenström 1992, Slagsvold and Dale 1996, Lind et al. 1999). The birds also suffer from a background mortality, M_b , which is independent of behaviour. Overall the probability of mortality per week which is unrelated to starvation is given by

$$M(u, r, oF, iF) = M_b + M_F u^2 (1 + 0.1r^2) / E(oF, iF) \quad (5)$$

where M_F is a parameter that scales the reserve-dependent predation hazard. Mortality acts during the week. Thus if a bird dies between t and $t + 1$, then any young that became independent at t are not affected, but any young that are still dependent at t die along with the parent bird.

Determination of the optimal strategy

The best strategy to adopt depends on the food availability $g(t)$. This strategy does not maximise the lifetime number of young produced by a bird. This is because young produced at some times of year are more likely to survive, and hence have greater reproductive value, than young produced at other times of year. Instead fitness is maximised by maximising the long-term rate of growth of descendant numbers (Metz et al. 1992), and can be found by dynamic programming (McNamara 1991, Houston and McNamara 1999).

Conversely, because there is density dependence, the strategy adopted by population members determines the food availability. To calculate g from the strategy we follow the population forward in time, starting with an initial specification of numbers of individuals in each state. Given such a population distribution at the start of week t , a measure of competition for food is determined. This then determines $g(t)$ for that week, and determines the population distribution at the start of week $t + 1$. This weekly updating is repeated until the food availability over the annual cycle converges so that it is the same in successive years.

We find the strategy that is the best given the food supply that is generated by a population following this same strategy. We refer to this self-consistent best strategy as the optimal strategy, but it is in fact

an evolutionarily stable strategy. To find the strategy and corresponding food availability we iterate over g ; we calculate the best strategy for a given g , and then update g to be the food availability generated when population members follow this strategy (Houston et al. 1988). This iterative procedure usually converges. This strategy specifies behaviour as a function of the bird's state and the time within the annual cycle. We call the behaviour that results from following the optimal strategy the optimal routine. Note that this behaviour is not necessarily the same in each year because of the way state variables change. For example, there may be year skipping, with a tendency to breed every alternate year.

To study the realised behaviour of the modelled birds we also run forward Monte Carlo simulations in which 10 000 birds follow the optimal strategy. The initial state distribution of the birds is the state distribution of newly fledged birds. In the simulation the birds use the food supply generated under the evolutionarily stable (i.e. optimal) strategy. Birds who have died are removed from the simulation and the descendants of the simulated birds are not entered into it. Results presented are for adults in a year at least two years after their birth and are based on birds that survive until the end of the year. By this time the influence of the initial state distribution at birth has disappeared.

In some exceptional cases (indicated on the figures) our procedure does not converge either because the population size oscillates or the best response is not unique. Note, however, that the magnitude of the oscillation or the difference between the best responses is small. Therefore, we also include these results.

Results

We first present our results for a baseline case and then investigate the effects of several parameters. To do so we will represent the events and their order under the optimal strategies with character strings using 'B' for a breeding attempt, 'i' for moult of the inner primaries and 'o' for moult of the outer primaries, so string 'Bio' means the birds first breed, then moult the inner primaries and finally moult the outer primaries.

The baseline case

The baseline values for the parameters (Table 1) represent the energetics of a medium-sized bird living in a seasonal environment. We also introduce an asymmetry between the two types of feathers assuming that the outer primaries have a greater effect on flight efficiency and their energetic cost of moult is higher (Table 1). The assumption of larger effects of outer primaries on flight efficiency is consistent with the fact that many birds reduce the speed of primary moult (by reducing the number of simultaneously growing feathers) when they moult outer primaries (Jenni and Winkler 1994). Since outer primaries are longer than inner ones (Jenni and Winkler 1994), the larger energetic cost to moult them seems to be reasonable.

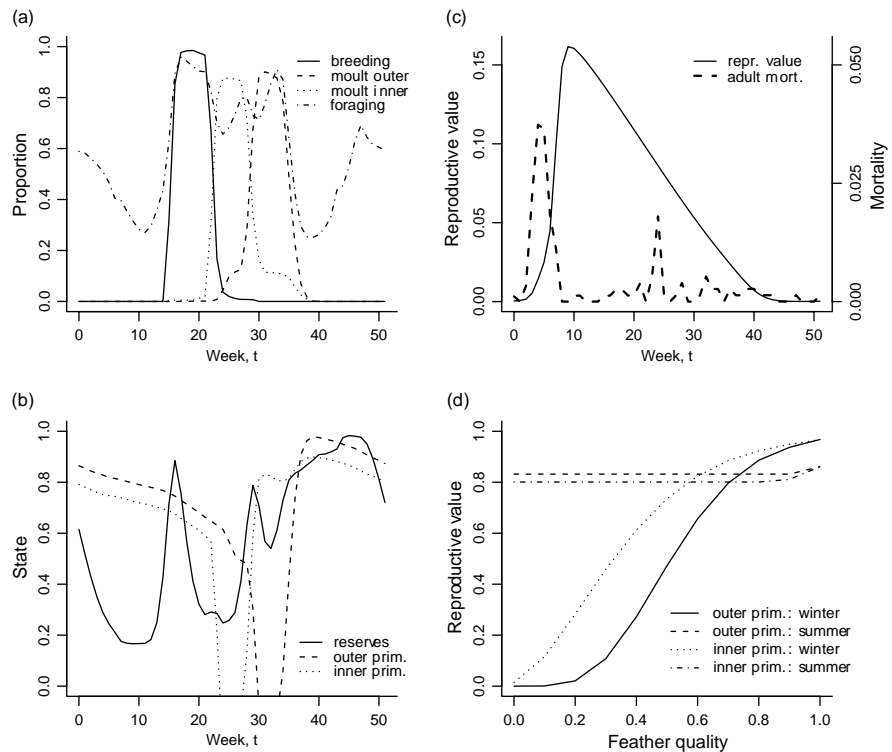
For the baseline case, birds following the optimal routine always breed before moult. The majority then moult inner primaries followed by outer primaries ('Bio', Fig. 1a). A small proportion (around 10%) moult outer primaries first and then the inner ones ('Boi'). Those who follow the 'Bio' pattern start to breed about a week earlier (at week 15.75 on average) than those who

Table 1. The model's parameters and their baseline values. Where two values are given the first one shows the value of outer primaries while the second one those of inner primaries. All energetic value given as the proportion of the bird's maximum fuel storage capacity.

Parameter	Symbol	Value	
Length of moulting period	j_m^{length}	6	6
The effect of foraging intensity on feathers' abrasion	j_f^f	0.018	0.018
The effect of feather quality on flight efficiency	j_δ	2	1
The interaction effect of feather quality on flight ability	$o_i \delta$	1	
The flight ability for very worn feathers	j_m^A	0.15	0.15
The description of feather quality effects	j_α	0.6	0.6
Energy cost of moulting feathers j	iK	0.6	0.55
The interaction cost of moulting both type of feathers	$o_i K$	0.35	
The extent of stochasticity in moult length	j^V	0.1	0.1
Cost of starting a new brood	Δ_s	1	
Gross intake needed to provide nestling	γ^{brood}	1.2	
Background mortality	M_b	0.0005	
Reserve dependent predation hazard	M_f	0.001	
Foraging efficiency of inexperienced birds	θ	0.75	
The extent of seasonality of food	ε	0.85	
The average amount of food available	A_{food}	1.55	
The maximal experience level	e_{max}	2	
Probability of increasing experience	p_e	0.025	
Maximum age of brood	a_{max}	7	
Number of female young at abandonment	n_{brood}	2	

Fig. 1. The baseline case.

(a) The behaviour of modelled birds as a function of time. (b) The average state of birds. When birds moult, feather qualities (dashed and dotted lines) fall below zero. (c) The reproductive value of the newly fledged young as function of time (solid line) and the proportion of individuals dying during a given week (dashed line). (d) The effect of feather quality on adults' reproductive value at $t=0$ (winter) and $t=26$ (summer).



follow the 'Boi' pattern (at week 16.77 on average). There are no differences in reserves and quality of inner primaries between the followers of different routines at week ten, but the quality of outer primaries differs; individuals with higher quality of outer primaries at week ten (0.81 vs 0.71) breed earlier and moult inner primaries first (pattern 'Bio'). Birds forage with high intensity during breeding and when moulting and with lower intensity during spring and autumn (Fig. 1a).

The reserves of the modelled birds peak just before breeding, then decrease sharply during breeding, rise again when the birds start moulting outer primaries and have the highest peak at the beginning of winter (Fig. 1b). The quality of feathers decreases continuously after moult. Birds do not wait to moult until the quality of their feathers abrades totally (i.e. $jF=0$), they moult with medium quality feathers (0.54 on average for both the outer and inner primaries).

Most of the deaths occur during late winter and midsummer (Fig. 1c), mainly as a result of starvation. The quality of feathers (both inner and outer primaries) of those birds who die in winter are lower than those who survive. The reproductive value of the newly fledged young is highest at the end of the winter but decreases steeply after that (Fig. 1c). Feather quality has a large effect on reproductive value in winter but has little effect in summer (Fig. 1d). Reproductive value in winter is very low unless the outer primaries are of reasonable quality (Fig. 1d).

The sequence of moult

As we have seen, the order of moult typically produced by our model (inner primaries first, followed by the outer ones) when there is significant seasonality agrees with the order found in many species (descendant primary moult or the basic sequence, Ginn and Melville 1983, Baker 1993). Still, our model shows considerable variation in the sequence of moult by members of a population.

In order to understand what attributes of the feathers influence the sequence of moult we first determine the optimal strategy and behaviour for completely symmetric feathers (i.e. each pair of feather parameters describing the same feature of the two types of primaries (i.e. each pair of feather parameters describing the same feature of the two types of primaries) and then we make feathers asymmetric, (introducing a difference between a given pair of parameters, so that their mean remains constant) and calculate the optimal strategy and behaviour again.

The results are shown in Table 2. With symmetric feathers the birds use both types of sequence ('io' and 'oi') more or less equally. Introducing asymmetry in the parameters which influence flight ability ($j\delta$, $j\alpha_A$, and $j\alpha$; Table 2) results in the baseline sequence of moult i.e. inner primaries moulted first and then outer primaries; sequence 'io' (Table 2). This means that feathers affecting flight ability to a greater extent should be moulted later. Changing the rate of abrasion ($j\beta$; Table 2) also results in the baseline routine, which reveals that feathers

Table 2. The effects of asymmetry in different feather parameters on the average starting date of moult of inner and outer primaries and the proportion of different moult sequences. Asymmetries were introduced so that the quality of outer primaries has the greater effect on flight ability, they abrade faster, or their energetic cost of moult is larger. For the line denoted by “none” the optimal strategy was determined for the baseline values (Table 1), except that parameters of feathers were equal to the means of values given in Table 1. The “difference” column gives the difference in value between the outer and inner primaries for the given parameter. The actual values of these parameters were such that their mean was equal to the baseline values. The feathers differed only in one parameter in each of these runs.

Symbol	Asymmetry		Time of moult of		Proportion of	
	Difference		inner prim.	outer prim.	‘io’	‘oi’
none	0		26.22	25.52	0.42	0.55
$j\delta$	1.4		23.11	29.08	0.93	0.05
j^m_A	0.14		23.58	27.97	0.87	0.1
$j\alpha$	0.6		23.64	28.45	0.89	0.07
j^f_r	0.005		23.73	28.42	0.89	0.07
j^k	0.21		28.99	24.15	0.06	0.92

abrading faster should be moulted later to keep them in good condition for the winter. The energetic cost of moult (j^k ; Table 2) has the opposite effect. Here feathers with higher energetic cost are moulted earlier, i.e. the order of moult is swapped compared to the baseline (sequence ‘oi’ instead of ‘io’). Apart from changes in the sequence, the annual routines were very similar to the baseline case.

Seasonal variation in food supply

We now study how environmental seasonality affects moult strategies. Given that tropical regions have less environmental seasonality, this might shed light on why moult strategies are more variable in the tropical zone than in the temperate zone. Since changing the seasonal variation ε for baseline parameter values rapidly leads to extinction of the population at extreme ε values (outside the range of 0.4–0.9), we investigate seasonal variation of food for a higher amount of food ($A_{\text{food}}=2.2$). Note, however, that the model with baseline food behaves similarly within the range where the birds survive.

When seasonality is very low ($\varepsilon \leq 0.05$), the birds follow a strategy which produces very variable behaviour in a given year (Fig. 2a, 3a–d). Many of the birds have a complete or incomplete moult before breeding (‘ioB’ and ‘iB’/‘oB’), while some of them do not breed at all, they just moult. A rather large proportion of birds follow other behaviours such as moult of inner primaries between two breeding attempts (‘BiB’), breeding between the moult of primaries (‘iBo’) or do not breed and moult at all. Breeding is delayed until the end of the favourable period of the year and moult of primaries mainly occurs before breeding (Fig. 2a, 2c, 3a–d). The proportion of birds that desert is very high under this condition while the adult mortality is low (Fig. 2d).

Under medium seasonality ($0.05 < \varepsilon < 1.2$), birds rarely have a complete moult and breed in the same year; when they breed they moult either no or just one type of primaries (Fig. 2a, 3e–h). Having a complete

moult but not breeding is also a common behavioural pattern. Our computations show that (i) moulting outer primaries and breeding rarely occur together in the same year and (ii) an individual’s behaviour in a given year influences its behaviour in the following year; those individuals who breed in one year usually skip breeding in the next year, while those who moult outer primaries usually skip this behaviour in the next year. As seasonality increases, the proportion of post-nuptial partial moult (e.g. ‘Bi’) gradually increases at the expense of the proportion of prenuptial partial moult (Fig. 2a). Nest desertion is still high under medium seasonality but it gradually decreases as seasonality increases (Fig. 2d).

When seasonality is high ($\varepsilon \geq 1.2$), the diversity of the routines is low; most of the birds have at least one breeding attempt and a complete postnuptial moult (Fig. 2a, 2c). Note, however, that there is variation within this basic type of routine. When seasonality is moderately high ($\varepsilon = 1.3$) the birds mainly follow the baseline routine ‘Bio’ (Fig. 3i). Increasing the seasonal variation of food from $\varepsilon = 1.3$ results in, first, an increase of the number of breeding attempts and a switch in the order of moult; outer primaries are moulted first (Fig. 3j). Increasing ε further leads to a large overlap between moults of inner and outer primaries (i.e. fast, simultaneous moult; Fig. 3k). Nest desertion rate is the lowest under high seasonality (Fig. 2d). Adult mortality, however, increases rapidly as seasonality becomes higher (Fig. 2d).

Birds forage most intensely during breeding and moult under all ε . Foraging intensity during winter, however, increases with increasing seasonality i.e. birds forage more intensely in seasonal environments (Fig. 3). The average number of breeding attempts has a minimum at intermediate seasonality (Fig. 2b).

To investigate the case of no seasonal variation we set $\varepsilon = 0$. In this case, birds breed and moult at any time of year following a variety of routines; their behaviour largely depends on the quality of their feathers: if the quality of both types of primaries is good, then they breed, otherwise they moult the primaries whose quality

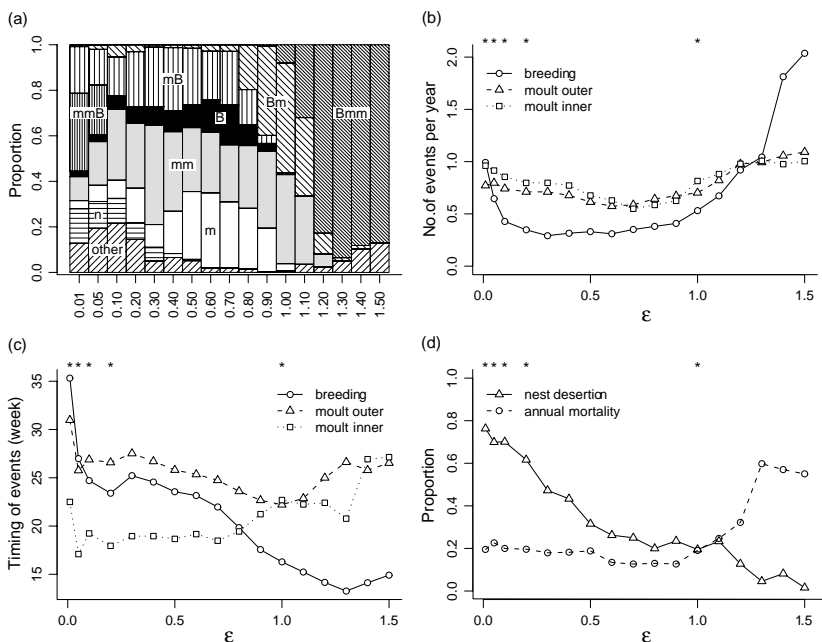


Fig. 2. The effects of seasonal variation of food, ϵ , on (a) the diversity of routines, (b) the average number of events, (c) the average timing of events, and (d) proportion of brood desertion and adult mortality. $A_{\text{food}} = 2.2$, all other parameters except ϵ were kept at their baseline values. The stars at the top of the panels mark those cases where no stable solution was found (i.e. the population cycles). In panel (a) for simplicity we ignored the order of moult and so 'm' and 'mm' mean an incomplete moult and a complete moult, respectively; 'n' indicates no breeding and moult in the given year, while the label 'other' covers complicated routines (e.g. 'BiB').

is lower. The rate of nest desertion is the highest under no environmental variation (Fig. 2d).

Food

Increasing the amount of food raises the density of birds through the year (Fig. 4a). Because the food per bird decreases with the density of birds, the average amount of food available for a forager ($g(t)$) changes little. On the other hand, its yearly pattern changes as the amount of food is increased; the more abundant the food supply is, the lower is its variation (Fig. 4b). As a consequence, the birds' optimal routines change with increasing amount of food in a way that is similar to how they change with decreasing seasonal variation (above). The routine that a bird follows is mainly determined by the quality of its feathers (Fig. 4c).

Decreasing the amount of food available for the birds from its baseline value – given that the birds receive enough food to survive – does not change the optimal routines; the birds follow the baseline routine 'Bio'.

Background mortality

We studied the effect of background mortality on optimal routines by varying M_b at different levels of

environmental seasonality, $\epsilon = 0.5, 0.9, 1.3$. Basically, the annual routines change in a way which results in more breeding under the more dangerous environmental conditions irrespective of ϵ . As M_b increases, the birds increase their number of breeding attempts (Fig. 5a). As a result, under low seasonal variation, they start to breed in every year instead of skipping breeding in some years (Fig. 5a), and, under high ϵ , they even have two breeding attempts (cf. McNamara et al. 2004). The proportion of breeding attempts that result in desertion, the time of first breeding (Fig. 5b), and the proportions of moults of outer and inner primaries all decrease. The speed of the moult (i.e. the overlap between the moult of the two types of feathers) and the degree of moult-breeding overlap also increase with raised background mortality.

Other parameters

To investigate the robustness of our model we ran many computations in which we changed the value of other input parameters (increase and decrease by ca 20% of their baseline values, one parameter at a time). We found that the alteration of the parameters θ , n_{brood} , N_0 , and M_f does not change the baseline optimal annual routine. Constant rate of feather abrasion (i.e. wear is independent of foraging intensity) also produces similar results.

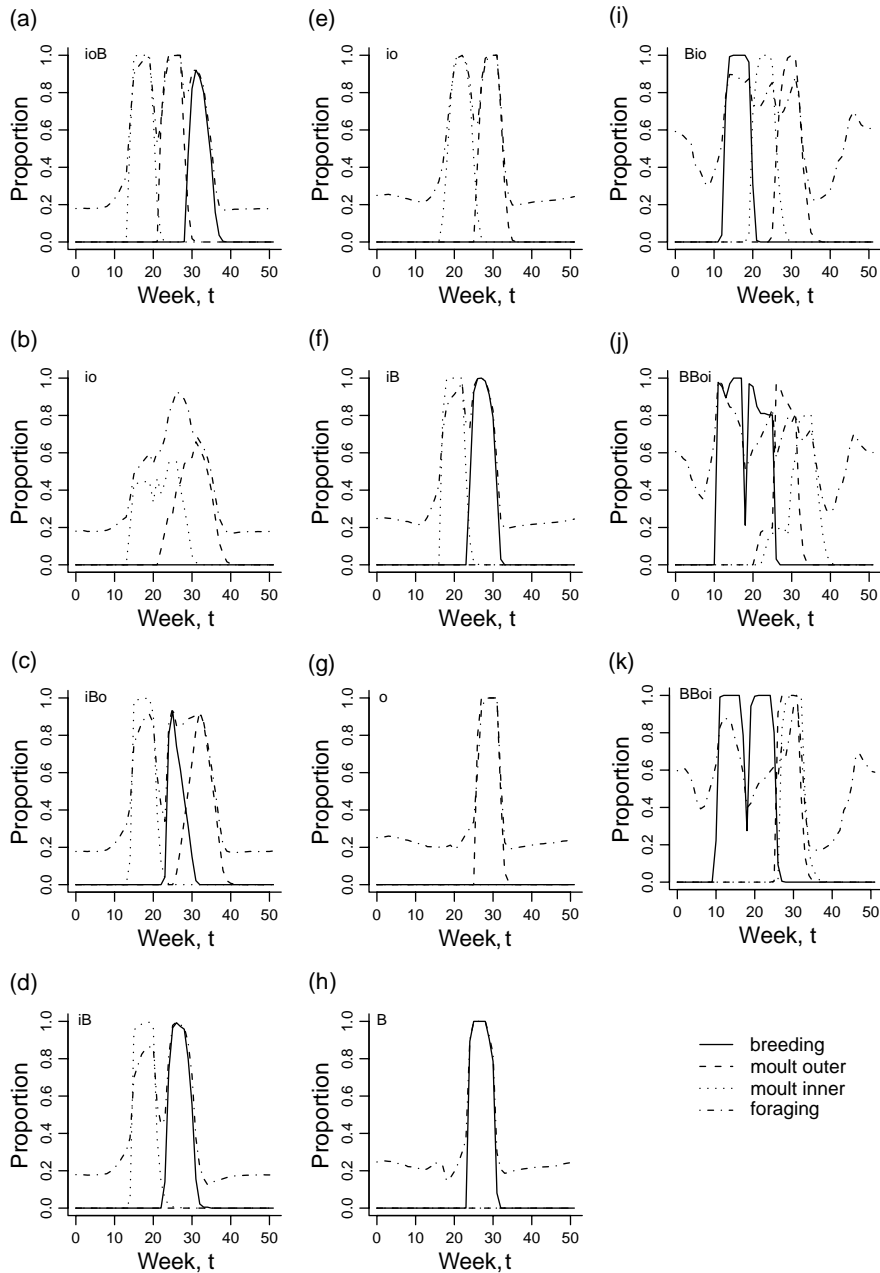


Fig. 3. An illustration of the variability of annual routines at different values of seasonality, ε . (a)–(d) and (e)–(h) the four most frequent routines when $\varepsilon = 0.05$ and $\varepsilon = 0.4$, respectively. (i), (j) and (k) the most frequent routines when $\varepsilon = 1.3$, 1.4, and 1.5. $A_{\text{food}} = 2.2$, all other parameters except ε were kept at their baseline values.

We will report the effects of physiological parameters (e.g. energetic costs) elsewhere.

Discussion

We have shown that environmental seasonality and life expectancy can affect life history parameters and annual

routines substantially. Our model predicts that if seasonality is high, a reduction in seasonality lowers breeding effort (measured as the number of breeding attempts) and adult mortality. At lower seasonality the effect of seasonality is minimal. The finding that birds living under low seasonality have lower breeding effort and mortality than birds living under high seasonality is in accordance with the well-established empirical results on the differences in life history traits between tropical and

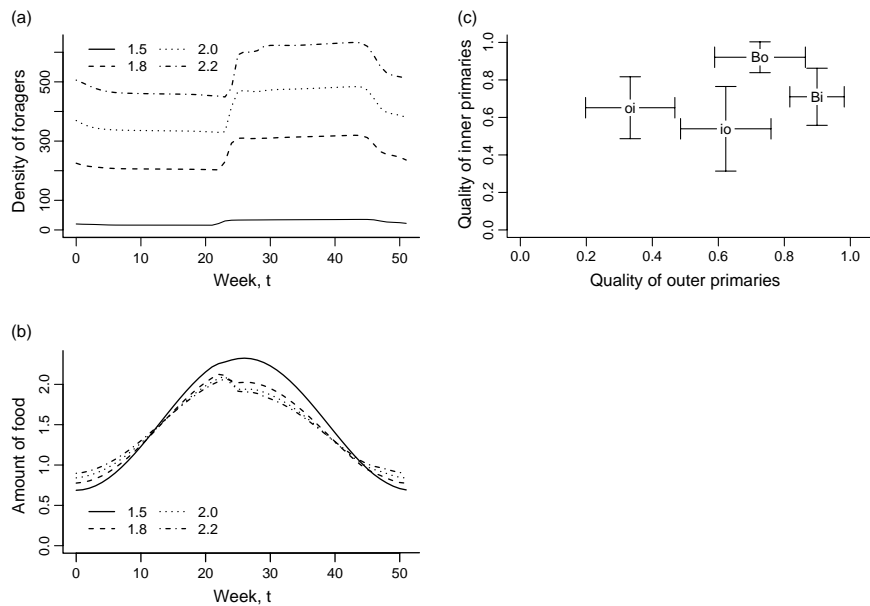


Fig. 4. The effects of increasing mean food supply A_{food} on (a) the density of foragers and (b) the amount of food available for a given individual $g(t)$. (c) The effect of the quality of feathers on the optimal routine when $A_{\text{food}} = 2.0$. The crosses of the horizontal and vertical error bars mark the average qualities of inner and outer primaries at week ten for individuals following different routines (denoted by the letters at the middle of the crosses). The error bars mark $\pm 1\text{SD}$. 'B' denotes breeding, 'i' denotes moulting inner primaries, and 'o' denotes moulting outer primaries. Parameters as in baseline case except the amount of food.

temperate birds (Skutch 1949, Lack 1968, Ricklefs 1969, 1980, Murray Jr. 1985, Martin 1996, Stutchbury and Morton 2001). Three major hypotheses try to explain these life history differences (Murray Jr. 1985, Martin 1996). The nest predation hypothesis assumes that birds in the tropics have low breeding effort and hence low mortality because they try to minimise the loss caused by the high level of nest predation (Skutch 1949, Martin 1996). The food limitation hypothesis states that birds have small clutches in the tropics because the small variation in the food supply allows only a limited surplus for reproduction during the tropical summer (Lack 1947, Ashmole 1963, Lack 1968, Ricklefs 1980). The adult survival hypothesis argues that low seasonality in the tropics leads to high adult survival which in turn selects for low reproductive effort (Murray Jr. 1985). It is still unclear which of these hypothetical effects is more important in shaping life histories (Martin 1996).

Our result emphasises the importance of the environmental seasonality in the food supply for the evolution of these life history differences and – since we did not vary predation hazard – shows that differences in nest predation risk are not necessary (Martin 1996). Our results based on changing environmental seasonality, ε , support the food limitation hypothesis, whereas our results based on changing background mortality, M_b , support the adult mortality hypothesis (for a fuller discussion of the effects of background mortality on annual routines of reproduction see McNamara et al. 2004). In our model, birds are able to control reproduc-

tive effort only by varying the number of reproductive attempts. A complete analysis, however, must allow clutch size to co-evolve with other aspects of the annual routine. We believe that extending the type of model we have presented here to include clutch size has tremendous potential for investigating these issues.

When the environment is seasonal our model predicts a slow (the moults of the two feather types do not overlap) and complete postnuptial moult, which is also the most common moult strategy found among temperate zone sedentary birds (Ginn and Melville 1983, Jenni and Winkler 1994) as well as among many tropical species (Payne 1980, Dittami and Gwinner 1985, Tidemann and Woinarski 1994, Wikelski et al. 2000). Several ecological factors may favour this type of annual routine. Environmental seasonality means the alternation of bad and good seasons (e.g. winter and summer or dry and rainy seasons), with reduced survival expectation for both adults and juveniles in the bad season. Early breeding then allows newly fledged young to gain enough experience to survive the winter. Late moult, on the other hand, means that feathers have less time to abrade before the harsh winter when feather quality is most important. The fact that feather quality counts less during breeding – when the conditions are good – also allows birds to moult just before the winter. In the baseline case the order of moult further supports this argument: birds moult those feathers (the outer primaries) later which have the larger effect on flight ability. This ensures that the quality of these feathers is higher

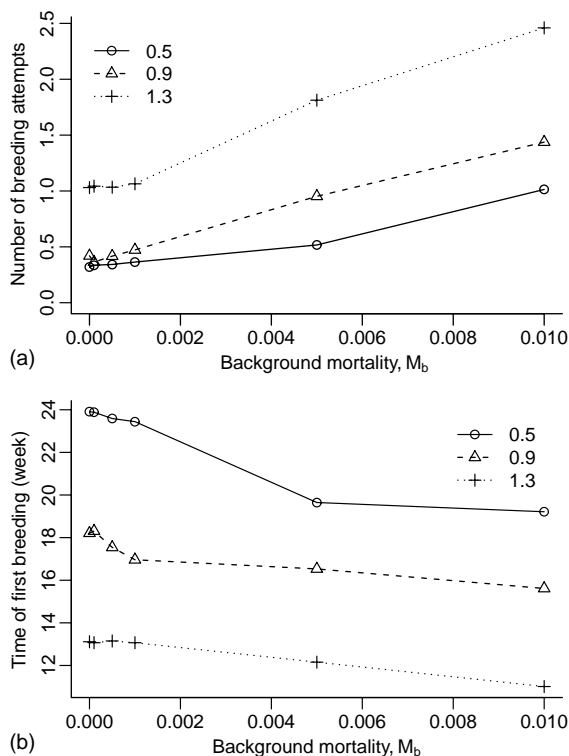


Fig. 5. The effects of increasing background mortality M_b on (a) the number of breeding attempts per year, and (b) the starting time of the first breeding attempt, in each case for three levels of seasonality, ($\epsilon = 0.5, 0.9, 1.3$). Other parameters are as baseline values. Averages were only calculated for birds surviving the whole year of the simulation.

during the winter than those of the less important inner primaries. This happens despite the fact that the energetic cost of the moult of the outer primaries is higher than that of the inner ones, i.e. from a purely energetic point of view it would be better to moult the outer primaries earlier when the food supply is more abundant. This higher energetic cost could explain why birds start to moult earlier when they can in our model. It also sheds light on why birds in our model switch the order of moult when they finish breeding late; keeping the baseline order 'io' in this case would mean that birds would need to perform the more energy-demanding moult when the food supply is low. If seasonality is very pronounced, modelled birds usually moult faster. This behaviour is well-documented for species at high latitudes (Holmes 1971, Earnst 1992, Hemborg et al. 2001). Moulting immediately after breeding is also the most common moult strategy for migratory bird species breeding in the temperate zone (Svensson and Hedenström 1999). This might be the result of phylogenetic inertia (e.g. migrants retain the ancestral moult strategy of non-migratory birds, Svensson and Hedenström 1999) or that postnuptial moult is still beneficial because of, for example, the advantages of having fresh flight

feathers available for autumn migration (Holmgren and Hedenström 1995).

Decreasing the seasonal variation in food results in harsher breeding condition in summer but milder winters, which improves survival and so makes breeding less urgent. As a consequence, it is optimal in our model to avoid breeding and the moult of both types of primaries during the same year. The resulting routine then is an alternation between breeding and moulting some of the primaries in one year and having a complete moult but no breeding in the other year. This result may, however, be a consequence of having no clutch size decision in our model, because the only way in which birds can reduce breeding effort is to skip breeding. It might be that, as seasonality decreases, real birds will first reduce clutch size instead of skipping as is widely reported for tropical birds (Lack 1947, Ricklefs 1980, Murray Jr. 1985). Consequently, in an environment where the food supply does not fluctuate significantly from year to year, one might expect skipping of breeding only in birds where clutch size cannot be further reduced i.e. in birds laying one egg per breeding attempts, like albatrosses.

The routines that our model has generated under low seasonality closely resemble those found in several species of albatrosses (Prince et al. 1993, Langston and Rohwer 1995, 1996). For instance, Prince et al. (1993) found that grey-headed albatrosses *Diomedea chrysostoma* (a species typically breeding only in every second year) moult on average 8.37 primaries (out of 10) in the year when they do not breed but only 2.97 primaries when they breed. Langston and Rohwer (1995) also describe a similar annual routine for the Laysan albatross *D. immutabilis* and the black-footed albatross *D. nigripes*. They found two distinct patterns of moult, namely a complete primary moult and an incomplete primary moult during which primaries of variable numbers and positions were replaced. Langston and Rohwer (1995) hypothesised that if birds finish a successful breeding attempt the moult is incomplete.

If seasonality is further reduced the modelled birds follow a large variety of annual behaviour, the most frequent of which is moult before breeding (prenuptial moult) because the food during summer is reduced to a level at which breeding only becomes possible with high quality feathers. On the other hand, the winter is so mild that birds can survive it with abraded feathers. This kind of annual schedule has been reported for the Seychelles fody *Foudia sechellarum* (Brooke 1985) and a couple of Sturnidae species living in South Africa (Craig 1983) but the majority of tropical species have postnuptial moult (Foster 1975, Stutchbury and Morton 2001). This discrepancy between the modelled and real birds might be caused by the temporal pattern of factors not included in the model (e.g. predation, Stutchbury and

Morton 2001) which may affect the relative timing of breeding and moult.

Only a very small seasonality (around 1% of the yearly average of food) is enough to maintain distinctly seasonal annual routines in our model. A similar effect has been found by McNamara et al. (2004). This might explain why birds follow a well determined seasonal schedule even at or close to the equator and under seemingly very uniform climatic conditions as both Ward (1969) (from Singapore, 1°20' N) and Fogden (1972) (from Sarawak, Borneo, 1°12' N) reported. Both authors describe some seasonal variation in the food supply despite the aseasonal climatic conditions, which, according to our model, might be enough to maintain the seasonal annual routines at these places. When no seasonal difference exist the modelled birds show rather irregular schedules, with moulting and breeding occurring in the population over the whole year. To our knowledge, only one field study reported a similar annual schedule for birds (Tallman and Tallman 1997) which might indicate the rareness of this condition.

By comparing the state variables of birds following different schedules we have shown that feather quality may have a strong influence on the organisation of annual routines. Birds with higher feather quality can breed earlier and/or more frequently than birds with more abraded feathers. According to our calculations, relatively small differences early in the year can greatly influence behaviour later. This prediction can be tested in the field by manipulating winter feather condition and then observing breeding behaviour in the next spring. Testing this prediction may illuminate the mechanism by which the cost of reproduction might operate (Nilsson and Svensson 1996). Furthermore, if it turned out that feather quality has a great influence on breeding behaviour and so on reproductive success, then monitoring quality could reveal valuable information about population processes.

Our model predicts that, under a seasonal environment, it may be optimal to moult different feather types at different times. Feathers with larger effects on flight ability, higher abrasion rate and lower energetic cost of moult should be moulted closer to the winter (i.e. later) than those with the opposite attributes. Since outer primaries are assumed to affect flight efficiency more (Jenni and Winkler 1994) and abrade faster than inner primaries (Baker 1993, Langston and Rohwer 1995) our model correctly predicts the sequence of moult that is most commonly found in nature (Ginn and Melville 1983, Baker 1993, Jenni and Winkler 1994). By doing so it offers a new explanation for why most birds renew their primaries descendantly: the sequence of moult may be an adaptive response to the problem of optimal timing of moult of differing feathers within the same feather tract. An extension of this argument may explain why the sequence of primary moult is stable and

the sequence of secondary moult is more variable. Primaries tend to differ from each other and so we would expect a well determined sequence of moult. In contrast, secondaries are more uniform and so it may be reasonable to expect that their order of replacement will be less regular across species.

It might be argued that the sequence of moult is simply a consequence of the physiological coupling of the replacement of feathers within the same feather tract. There are, however, many observed exceptions to this strict sequence (Baker 1993, Jenni and Winkler 1994) which makes this physiological constraint implausible. Nevertheless, in most of our computations the two types of primaries were moulted immediately after each other despite the fact they were not coupled.

It follows from the above argument that individual variation in the sequence of moult can be an adaptive response to some unusual environmental conditions or changes in internal state (e.g. malnutrition or disease). We suggest that detailed studies of these variations may help to improve our understanding of the evolutionary forces behind moult strategies.

To conclude, we have investigated several aspects of the annual schedules of non-migratory birds with a self-consistent state-dependent optimal annual routine model. By changing seasonality our model successfully generates a wide variety of moult sequences found in nature. Furthermore, by introducing two feather types we were able to offer a new explanation for why birds generally moult their primaries descendantly. Future directions of investigation should include the effect of physiology and migration on moult strategies. Also, to study life history differences between tropical and temperate birds future models should allow the clutch size to be optimised.

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The Appendix O14240 can be found at
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