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Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis

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ABSTRACT

Birds display a latitudinal gradient in clutch size. Ashmole's hypothesis explains this geographic pattern by differences in seasonality of resources resulting in different levels of winter mortality. Ashmole assumed that populations are strongly limited by resources during the non-breeding season, and the level of resources available in the breeding season relative to the non-breeding season determines clutch size. The main problem with Ashmole's hypothesis is that it does not take into consideration trade-offs of reproduction. Applying a simulation approach and concepts of life-history theory, we therefore re-evaluate the hypothesis. In particular, we analyse four alternative mechanisms that may generate a gradient in clutch size: (1) differences in levels of seasonality of resources causing winter mortality and no cost of reproduction (= Ashmole's hypothesis); (2) differences in levels of seasonality of resources and a cost of reproduction that may act on juveniles and/or adults; (3) no differences in levels of seasonality of resources but there is a cost of reproduction; and (4) no differences in levels of seasonality of resources and no cost of reproduction. To model cost of reproduction, three general cost functions were assumed: linear, hyperbolic or exponential decrease in future survival of individuals for increasing clutch sizes. Whereas the mechanisms implemented in alternatives (1), (3) and (4) did not generate a gradient in clutch size, those given in alternative (2) were able to generate this pattern. This suggests that Ashmole identified seasonality of resources as one important mechanism for geographic variation in clutch size, but did not recognize cost of reproduction as a second mechanism. In particular, we observed the gradient in our simulations in two situations: (i) linear or hyperbolic cost of reproduction for offspring and no costs for parents; and (ii) linear or hyperbolic cost of reproduction for offspring together with any type of cost of reproduction for parents. In these situations, widely accepted differences and correlations among life-table variables of tropical and temperate avian species did hold. Our results are valid for a wide range of geographic clutch size variation that may be the result of adaptation to seasonal environments.

Keywords: clutch size, cost of reproduction, density dependence, fecundity, seasonality of resources, survival, tropical *vs* temperate.

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INTRODUCTION

Latitudinal gradients have intrigued ecologists because of their general occurrence. Species diversity, the degree of specialization of organisms and annual productivity decrease from the equator towards the poles (for a review, see Cardillo, 2002). Geographic variation in life histories has also been documented for many species. For example, in birds, tropical species differ from temperate species in several aspects of their life histories. Tropical species lay smaller clutches, have longer development periods, have extended parental care leading to higher juvenile survival and have higher adult survival than their temperate counterparts (for a review, see Murray, 1985; Skutch, 1985; Martin, 1996; Ricklefs, 2000).

To understand the evolution of clutch size and its geographic patterns, ornithologists have approached offspring number from life-history theory. The life history of an organism can be viewed as an adaptation to environmental conditions and presents a solution to the problem of optimizing reproductive schedules under constraints. Two classes of trade-offs (Stearns, 1992) that counteract infinite reproductive rates by causing a cost of reproduction ('Darwinian demons'; Law, 1979) can be distinguished: trade-offs that operate between the parent and the offspring (inter-generational trade-offs) and those operating within one individual (intra-individual trade-offs). According to the concept of inter-generational trade-offs, a parent balances the benefit that it obtains from the current reproductive effort and the cost of this effort as reflected in reduced future fecundity. In contrast, according to the existing intra-individual trade-offs of reproduction, each female lays that number of eggs which maximizes the number of offspring recruited into the breeding population (Lack, 1947). The clutch size reflects the availability of food resources, the territory quality available to parents or their ability to rear offspring. Based on these concepts, the latitudinal gradient in clutch size is the result of a gradient in environmental conditions (availability of food resources for Lack, 1947; nest predation for Skutch, 1949, 1967) or in the amount of inter-generational trade-offs (life-time for Martin *et al.*, 2000). Consequently, many studies have tried to demonstrate differences in trade-offs between the tropics and the temperate region to explain small avian clutches in the tropics.

For many bird species, the cost of reproduction assumed by life-history theory has been demonstrated in brood manipulation experiments (reviewed in Stearns, 1992; Norris *et al.*, 1994; Siikamaki *et al.*, 1994; Fargallo and Merino, 1999; Golet and Irons, 1999; Hemborg, 1999; Tavecchia *et al.*, 2001; Veasey *et al.*, 2001; Orell and Belda, 2002). These experimental studies have shown that survival of juveniles and/or adults decreases with increasing clutch size. Several other experiments have failed to demonstrate costs within the observation period (for a review, see Stearns, 1992; Blondel *et al.*, 1998; Murphy *et al.*, 2000; Johannesen *et al.*, 2003). However, to satisfactorily demonstrate cost of reproduction, brood-manipulation experiments together with long-term monitoring of the fate of offspring and their parents are required. Therefore, the most obvious reasons for failing to demonstrate cost of reproduction experimentally are an insufficient observation period that does not cover long-term consequences of brood-manipulation in the field (Golet and Irons, 1999; Veasey *et al.*, 2001; Orell and Belda, 2002) and problems with monitoring individuals.

Adaptations express the evolutionary modification of the gene pool of a population to the environment, which includes individuals of other species, the same species and abiotic conditions. As a consequence, density-dependent processes that affect the population have a feedback on life-history patterns, since they also modify a population's gene pool. Ashmole (1963) noted this influence of density-dependent mortality factors on the evolution of avian clutch size. He stated that populations are strongly limited by resources during the non-breeding season, and the level of resources available in the breeding season relative to the non-breeding season determines clutch size. Following this insight, for habitats with low levels of seasonality of resources such as the tropics, low clutch sizes are expected, whereas higher clutch sizes are favoured in temperate habitats that are characterized by higher levels of seasonality resulting in high levels of winter mortality (Ashmole's hypothesis; Ashmole, 1963). Based on life-history theory, the main problem with Ashmole's (1963) hypothesis is that it does not assume a cost of reproduction, which opposes the existence of infinitely large clutch sizes (Law, 1979).

In this paper, we consider under which assumptions differences in seasonality of resources can select for different clutch sizes. We analyse four principal alternative mechanisms that may give rise to a latitudinal gradient in clutch size:

1. Differences in levels of seasonality of resources and no cost of reproduction (= Ashmole's hypothesis; Ashmole, 1963).
2. Differences in levels of seasonality of resources and a cost of reproduction that may act on juveniles (intra-generational trade-off) and/or adults (inter-generational trade-off).
3. No differences in levels of seasonality of resources but there is a cost of reproduction.
4. No differences in levels of seasonality of resources and no cost of reproduction.

We also assume that seasonality of resources causes winter mortality and thus influences the reproductive rate through its density-dependent effect on food supply.

As a first step to understand tropical and temperate avian clutch size, we focus on single-brooded species. Thus, the results presented in this paper are mainly applicable to birds in the families *Strigidae, Accipitridae, Falconidae* and *Corvidae* and only to some Passeriformes. Considering multiple-brooded birds is considerably more complex because the effect of the length of the breeding season on clutch size has to be included. During a year tropical species have more months that have suitable conditions to rear their offspring than temperate species. Moreover, it has been shown that fledglings from early nests are more likely to be recruited as breeders in the population than fledglings from later nests (Brown and Roth, 2002).

To derive which mechanisms given by alternatives (1) through (4) select for a gradient in clutch size, we developed an individual based model (Kaiser, 1979; DeAngelis and Gross, 1992) in the present study. In cases where a linear-like gradient in clutch size builds up in our simulations, we analyse whether these situations are applicable to natural bird populations and whether widely accepted differences and correlations among life-table variables of tropical and temperate birds hold (Ricklefs, 1997, 2000). Finally, we discuss how our results can explain a wide range of geographic clutch size variation.

MATERIALS AND METHODS

The model

We developed an individual based model (Kaiser, 1979; DeAngelis and Gross, 1992; Griebeler and Seitz, 2002) for a population evolving its clutch size. The strategic model (May, 1986) distinguishes two types of individuals: juveniles and adults. Each individual owns a genotype that determines its clutch size. The number of eggs laid by adults is coded by this genotype and ranges from 1 to 10 eggs.

The length of one time step for the model was considered to be one generation. A generation equals the breeding season plus the non-breeding season and starts with reproduction of adults in the breeding season. Assuming a 1 : 1 sex ratio, one-half of the adults give offspring according to their genotype and they transmit their genotype to each of their offspring. The other half of the population is implicitly assigned as partners of these reproducing individuals. Since only one parent transmits its genotype to offspring, the choice of mates implemented in our model corresponds to strong positive assortative mating. For the reasons described above, we focus on single-brooded birds, and thus reproduction occurs only once during the breeding season. Juveniles that have passed the breeding season and the subsequent non-breeding season are treated as adults in the following year.

Seasonal variation in resources

To implement the mechanism seasonal variation in resources assumed for alternatives (1) and (2), we presumed two carrying capacities limiting resource availability for the population. Parameter K_{Summer} models availability of resources during the breeding season in summer and K_{Winter} those during winter, the period between one breeding season and the next. Thus, population size is limited twice in our model, once in the breeding season and once in the non-breeding season. The limitation in the non-breeding season corresponds to Ashmole's winter mortality resulting from a decrease in food availability from summer to winter, whereas the limitation in summer models availability of food during the breeding season. If the total population size N is higher than K_{Summer} in the breeding season (K_{Winter} in the non-breeding season), $N - K_{\text{Summer}}$ individuals ($N - K_{\text{Winter}}$ individuals) will die at the end of the breeding season (non-breeding season). In both seasons, both juveniles and adults suffer from these mortalities caused by food availability. The probability that a specific juvenile (adult) dies in one of these periods is primarily proportional to the frequency of juveniles (adults) in the population, but will be modified if a cost of reproduction is assumed (for alternatives 2 and 3, see below).

No seasonality in resources (alternatives 3 and 4) is modelled as $K_{\text{Summer}} = K_{\text{Winter}}$. In this special case of seasonality, population size is in fact only limited once after the breeding season.

Cost of reproduction

For alternatives (2) and (3), we assumed two types of cost of reproduction that may affect the population during a generation: costs for offspring and costs for parents. These costs are implemented as differences in survival probabilities between genotypes and express intra-individual trade-offs and inter-generational trade-offs, respectively. For alternative (2) where $K_{\text{Summer}} > K_{\text{Winter}}$, costs take effect on juveniles only through summer mortality and impact adults only through winter mortality. In contrast, for $K_{\text{Summer}} = K_{\text{Winter}}$ (alternative 3), costs take effect on both life-stages after summer because population size is only limited once within a generation. With no cost of reproduction assumed for juveniles and/or adults, a specific individual dies during the ceiling of population size in summer/winter proportional to the frequency of its life-stage in the population. If a cost of reproduction is assumed, the probability that a specific juvenile/adult dies is no longer simply proportional to the frequency but is modified according to its genotype. For juveniles, this means that offspring from larger clutches die with a higher probability than offspring from smaller clutches (intra-individual trade-off). For adults, parents that laid more eggs in summer and thus experienced a higher cost of reproduction die with a higher probability than those that had smaller clutches (inter-generational trade-off). To model genotype-dependent cost of reproduction for each life-stage as differences in survival probabilities, we chose each of the three general functions (Fig. 1) described by Pearl and Minor (1935). These functions implement a hyperbolic, linear or exponential increase in cost of reproduction for an increasing clutch size and give the relative differences in chance of survival for juveniles (in summer) and for adults (in winter if $K_{\text{Summer}} > K_{\text{Winter}}$, or in summer if $K_{\text{Summer}} = K_{\text{Winter}}$) in dependence of clutch size during the ceiling of population size.

Restricting cost of reproduction for juveniles to summer and for adults to winter contradicts a variety of studies linking nestling condition to their winter mortality or adult summer mortality to clutch size, respectively. However, an additional simulation study that was analogous to the study presented here, but which allowed for cost of reproduction acting in summer and winter on both juveniles and adults, showed that our results are not affected by this simplification of the model. The scenarios where a latitudinal gradient was observed in the simpler model were also obtained when both life-stages were affected by costs in both seasons and vice versa. Clutch sizes estimated in these scenarios for a specific latitude differed only slightly (± one egg). Therefore, in this paper we present only the results obtained for the simple model which restricts cost of reproduction for juveniles to summer and for adults to winter.

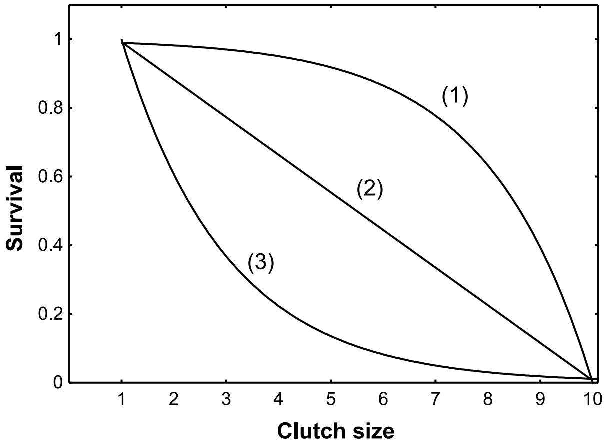

Fig. 1. Functions assumed for cost of reproduction. For alternatives (2) and (3), cost functions are used for juveniles (CJ) and adults (CA), respectively. Cost is implemented as survival of juveniles and adults, respectively. Survival decreases hyperbolically (Type 1), linearly (Type 2) or exponentially (Type 3). Functions used are: (1) $\text{survival}(\textit{clutch size} - 1) = 1 - \exp(-0.5 \times (10 - \textit{clutch size}))$; (2) $\text{survival}(\textit{clutch size} - 1) = \frac{y_p - 1}{x_p}(\textit{clutch size} - 1) + 1$, where (x_p, y_p) is the point of intersection of functions (1) and (3); and (3) $\text{survival}(\textit{clutch size} - 1) = \exp(-0.5 \times (\textit{clutch size} - 1))$. Cost functions give the relative chance of survival dependent on clutch size during limitation of population size in summer and in winter.

Computer simulations

To determine which mechanisms account for the latitudinal gradient in clutch size, we performed a simulation study for each alternative.

Seasonal variation in resources

Applying the NDVI (normalized difference vegetation index) as a predictor of seasonal production, Hurlbert and Haskell (2003) recently found that summer production exhibits no gradient with latitude, whereas winter production is lower and shows a decrease with increasing latitude. Based on their observation, we assumed $K_{\mathrm{Summer}} > K_{\mathrm{Winter}}$ in our simulations for alternatives (1) and (2) to model seasonality of resources. For these two alternatives, the simulations were always started at summer capacity with 1000 adults at the beginning of the breeding season and K_{Winter} ranged from 700 to 1000 adults. For alternatives (3) and (4) with no seasonality of resources, K_{Summer} always equalled K_{Winter} and ranged from 700 to 1000 adults to study the potential influence of the resource level *per se*. Again simulations of populations were started at summer capacity at the beginning of the breeding season. The simulations performed for alternatives (3) and (4) test the two alternative hypotheses that the latitudinal gradient in summer production representing resource availability during the breeding season accounts, with or without a cost of reproduction, for the latitudinal gradient in clutch size and not the difference between the summer and winter level (Ashmole, 1963).

Cost of reproduction

For the two alternatives (2) and (3) where a cost of reproduction was assumed, we distinguished three general combinations (Table 1): costs for both juveniles and adults (CJ and CA), costs for juveniles but no costs for adults (CJ and ¬CA) and no costs for juveniles but costs for adults (¬CJ and CA). Combination (CJ and CA) allows us to study the effect of trade-offs acting on both juveniles and adults for these two alternatives. Combinations (CJ and ¬CA) and (¬CJ and CA), however, enable us to rate the individual effect of cost of reproduction for juveniles and adults, respectively.

Table 1. Cost scenarios studied for alternatives (2) and (3)

Cost of reproduction	Cost functions assumed
CJ and ¬CA	CJ: $\mathrm{CJ}_{\mathrm{linear}}$, $\mathrm{CJ}_{\mathrm{hyperbolic}}$ or $\mathrm{CJ}_{\mathrm{exponential}}$ ¬CA: survival independent of clutch size
¬CJ and CA	¬CJ: survival independent of clutch size CA: $\mathrm{CA}_{\mathrm{linear}}$, $\mathrm{CA}_{\mathrm{hyperbolic}}$ or $\mathrm{CA}_{\mathrm{exponential}}$
CJ and CA	CJ: $\mathrm{CJ}_{\mathrm{linear}}$, $\mathrm{CJ}_{\mathrm{hyperbolic}}$ or $\mathrm{CJ}_{\mathrm{exponential}}$ CA: $\mathrm{CA}_{\mathrm{linear}}$, $\mathrm{CA}_{\mathrm{hyperbolic}}$ or $\mathrm{CA}_{\mathrm{exponential}}$

Note: Cost of reproduction for juveniles (CJ), no cost of reproduction for juveniles (¬CJ), cost of reproduction for adults (CA) and no cost of reproduction for adults (¬CA). For CJ and CA, we chose each of the three general functions given in Fig. 1 for survival (linear, hyperbolic, exponential). If no cost of reproduction is assumed, the survival of life-stages (¬CJ, ¬CA) is proportional to the frequency of the life-stage in the population.

It should be noted that if seasonality of resources is assumed, the missing combination (¬CJ and ¬CA) is equivalent to alternative (1), and thus corresponds to Ashmole's hypothesis (Ashmole, 1963). In contrast, if no seasonality in resources is assumed, (¬CJ and ¬CA) corresponds to alternative (4).

Searching for the optimal clutch size

To derive the genotype with the best fitness for each simulation experiment, we performed 100 repeated Monte-Carlo simulations of 500 generations and looked for the genotype with the highest frequency. Genotypes of clutch size ranging from 1 to 10 offspring were uniformly distributed in the initial population to give each clutch size an equal chance of prevailing. Any other distribution of genotypes (e.g. normal distribution) would promote specific genotypes at the beginning of the adaptation process. This will not change the optimal clutch size finally obtained, but will influence the time needed by the model to stabilize at the optimal size. If genotypes with higher frequencies are already well-adapted, stabilization time will be shortened; however, when they are poorly adapted, more generations are needed to stabilize than for the equally distributed clutch sizes. Starting with the population consisting of uniformly distributed genotypes, we simulated 500 generations. At the end of these generations, the frequency for each of the ten genotypes that initially existed in the population was calculated. To investigate whether a clutch size is an evolutionarily stable strategy, mutation occurred after each simulated generation. The probability that any adult individual randomly changed its genotype to any other genotype during one generation was 10^{-3}, resulting on average in about one mutant per generation. Consequently, in most simulations no genotype was fixed after 500 generations, but the frequencies of the non-fittest genotypes were always in the range of the mutation rate assumed and genotypes were approximately normally distributed as expected from nature.

Calculation of life-table variables for the optimal clutch size

To test the validity of widely accepted empirical gradients in life-table variables and correlations between life-table variables (Ricklefs, 1997, 2000), we performed each simulation experiment for the search of the optimal clutch size again, but the simulations were initialized with homogeneous populations consisting of individuals with the optimal genotype found in the respective experiment. Mutation was disabled in these simulations. During these Monte-Carlo simulations, we recorded the annual survival rate of juveniles (l_j), the annual adult survival rate (l_a), the mean life-time of an individual (m) and the fecundity (f), which we defined as the number of surviving juveniles per generation and per adult. We analysed life-table variables for the fittest genotype in each simulation experiment because we expect this genotype to dominate in nature under the respective conditions.

Adjustment of ($K_{\text{Summer}}/K_{\text{Winter}}$) to latitude

To link the ratio in summer and winter capacity to latitude needed for alternatives (1) and (2), we searched for data sets obtained at different latitudes which could reveal ratios for carrying capacities of birds in summer and in winter. The field studies of Bauer *et al.* (1995) give such a ratio for the temperate region. These authors estimated the mean breeding population size of the 50 most common bird species during the winters 1987/88–1991/92 and the corresponding summers in Baden-Württemberg, Germany. From this source, we summed breeding sizes of all land birds for summer and winter, respectively, and obtained for Baden-Württemberg 1.35 as the ratio of summer and winter capacity. This shows that in our simulation experiments, the parameter combination $K_{\text{Winter}} = 750$ and $K_{\text{Summer}} = 1000$ corresponds to a latitude of about 48°. For the tropics, however, we could not find such data and, therefore, assumed 1.01 as the ratio. The latter ratio results from a difference of 10 individuals in summer and winter capacity, which we assumed to represent low seasonal variation of resources in the humid tropics ($1000/990 = 1.01$). The data point set for the tropics and the ratio of 1.35 derived for 48° latitude together map ($K_{\text{Summer}}/K_{\text{Winter}}$) to latitude.

RESULTS

Searching for the optimal clutch size

In all simulation experiments where no trade-offs of reproduction were supposed (alternatives 1 and 4), the genotype with the maximal clutch size (10) did always prevail in our simulation experiments. This outcome was independent of whether seasonality in resources was assumed (alternative 1) or not (alternative 4). Consequently, under alternatives (1) and (4) no gradient in clutch size was observed and Ashmole's hypothesis (1) was not confirmed.

In the simulation experiments for alternative (3), where no seasonality in resources but a cost of reproduction were assumed, the fittest genotype did not depend on the value assumed for K_{Summer} but depended strongly on the cost combination and the cost function assumed. The maximal clutch size did always prevail in cost combination ($\neg$CJ and CA). A clutch size of one was found in seven cases: ($CJ_{\text{exponential}}$ and $\neg$CA), (CJ_{linear} and CA_{linear}), (CJ_{linear} and $CA_{\text{exponential}}$), ($CJ_{\text{hyperbolic}}$ and CA_{linear}), ($CJ_{\text{hyperbolic}}$ and $CA_{\text{exponential}}$), ($CJ_{\text{exponential}}$ and CA_{linear}) and ($CJ_{\text{exponential}}$ and $CA_{\text{exponential}}$). Two eggs were best in four cases: (CJ_{linear} and $\neg$CA), (CJ_{linear} and $CA_{\text{hyperbolic}}$), ($CJ_{\text{hyperbolic}}$ and $CA_{\text{hyperbolic}}$) and ($CJ_{\text{exponential}}$ and $CA_{\text{hyperbolic}}$), whereas three eggs were found only for ($CJ_{\text{hyperbolic}}$ and $\neg$CA). In summary, the resource level *per se* did not account for a latitudinal gradient in clutch size. For all cost combinations and all cost functions investigated, differences in resource levels did not cause differences in optimal clutch sizes.

In contrast, for alternative (2), we found eight scenarios out of 15 that were tested for which an increase in the difference in seasonality of resources resulted in a linear-like increase in the optimal clutch size (Table 2). In particular, there were two situations under which a latitudinal gradient in clutch size builds up: (1) linear or hyperbolic cost of reproduction for offspring and no costs for parents; and (2) linear or hyperbolic cost of reproduction for offspring together with any type of cost of reproduction for parents. If no costs for juveniles were assumed and costs for parents were present, the maximal clutch size did always prevail independent of the type of cost function assumed for parents. In the remaining four cases of a total of 15 cost scenarios (Table 1), ten eggs were optimal again if $K_{\text{Summer}} > K_{\text{Winter}}$ was assumed.

Calculation of life-table variables for the optimal clutch size

We restricted the simulation experiments performed for the life-table variables of individuals expressing the optimal clutch size to the eight scenarios where a latitudinal gradient in clutch size was observed. These simulations revealed that the annual juvenile survival rate, the annual adult survival rate and the mean life-time of an individual

Table 2. Optimal clutch sizes estimated under alternative (2)

	Clutch sizes estimated $K_{\mathrm{Summer}}/K_{\mathrm{Winter}}$							
Cost scenario	1.00	1.01	1.07	1.14	1.23	1.33	1.45	1.60
$\mathrm{CJ}_{\mathrm{linear}}$ and ¬CA	**2**	**2**	**3**	**4**	**4**	**5**	**5**	**6**
$\mathrm{CJ}_{\mathrm{hyperbolic}}$ and ¬CA	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**
$\mathrm{CJ}_{\mathrm{exponential}}$ and ¬CA	1	1	10	10	10	10	10	10
¬CJ and $\mathrm{CA}_{\mathrm{linear}}$	10	10	10	10	10	10	10	10
¬CJ and $\mathrm{CA}_{\mathrm{hyperbolic}}$	10	10	10	10	10	10	10	10
¬CJ and $\mathrm{CA}_{\mathrm{exponential}}$	10	10	10	10	10	10	10	10
$\mathrm{CJ}_{\mathrm{linear}}$ and $\mathrm{CA}_{\mathrm{linear}}$	**1**	**1**	**3**	**4**	**4**	**4**	**4**	**5**
$\mathrm{CJ}_{\mathrm{linear}}$ and $\mathrm{CA}_{\mathrm{hyperbolic}}$	**2**	**2**	**3**	**4**	**4**	**4**	**4**	**4**
$\mathrm{CJ}_{\mathrm{linear}}$ and $\mathrm{CA}_{\mathrm{exponential}}$	**1**	**1**	**3**	**4**	**4**	**5**	**5**	**6**
$\mathrm{CJ}_{\mathrm{hyperbolic}}$ and $\mathrm{CA}_{\mathrm{linear}}$	**1**	**1**	**3**	**3**	**3**	**3**	**4**	**4**
$\mathrm{CJ}_{\mathrm{hyperbolic}}$ and $\mathrm{CA}_{\mathrm{hyperbolic}}$	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**4**
$\mathrm{CJ}_{\mathrm{hyperbolic}}$ and $\mathrm{CA}_{\mathrm{exponential}}$	**1**	**1**	**3**	**3**	**3**	**4**	**4**	**4**
$\mathrm{CJ}_{\mathrm{exponential}}$ and $\mathrm{CA}_{\mathrm{linear}}$	1	1	10	10	10	10	10	10
$\mathrm{CJ}_{\mathrm{exponential}}$ and $\mathrm{CA}_{\mathrm{hyperbolic}}$	2	2	10	10	10	10	10	10
$\mathrm{CJ}_{\mathrm{exponential}}$ and $\mathrm{CA}_{\mathrm{exponential}}$	1	1	10	10	10	10	10	10

Note: Alternative (2) assumes seasonality in resources and cost of reproduction. Scenarios where clutch size increases linear-like with increasing ratios of summer and winter capacity are shown in **bold**. The quotient $K_{\mathrm{Summer}}/K_{\mathrm{Winter}}$ models the amount of seasonality of resources; 1.01 corresponds to the tropics and 1.35 to Baden-Württemberg, Germany (48° latitude). It should be noted that column $K_{\mathrm{Summer}}/K_{\mathrm{Winter}} = 1000/1000 = 1.00$ means no seasonality of resources together with a cost of reproduction (alternative 3).

decreased with increasing ratios in summer and winter capacity (Table 3). Annual fecundity of adults (f), defined as the number of offspring per adult that grow up to adults per generation (= clutch size × l_j), increased with increasing differences in capacities ($K_{\mathrm{Summer}} - K_{\mathrm{Winter}}$) or increasing ratios $K_{\mathrm{Summer}}/K_{\mathrm{Winter}}$, respectively (Table 3). Annual fecundity was thus obviously inversely proportional to annual adult survival.

DISCUSSION

Assuming an increase in seasonality of resources from the poles to the equator and trade-offs of reproduction (alternative 2), we found eight scenarios out of 15 that were tested in which a linear-like latitudinal gradient in clutch size builds up. These scenarios could be classified as follows: (1) linear or hyperbolic cost of reproduction for offspring and no costs for parents; and (2) linear or hyperbolic cost of reproduction for offspring together with any type of cost of reproduction for parents. Under these conditions, differences in seasonality of resources select for differences in clutch size and the level of clutch size depends on the ratio of the two resource levels. If juveniles and adults have no cost of reproduction and

Table 3. Annual adult survival rate (l_a), mean life-time of an individual (m) and annual fecundity (f) in relation to ratio of summer and winter capacity

	$K_{\text{Summer}}/K_{\text{Winter}}$																							
	1.00			1.01			1.07			1.14			1.23			1.33			1.45			1.60		
Cost scenario	l_a	m	f	l_a	m	f	l_a	m	f	l_a	m	f	l_a	m	f	l_a	m	f	l_a	m	f	l_a	m	f
CJ_{linear} and ¬CA	0.50	2.0	1.0	0.50	2.0	1.0	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.29	1.4	1.4	0.29	1.4	1.4	0.25	1.3	1.5
$CJ_{\text{hyperbolic}}$ and ¬CA	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3
CJ_{linear} and CA_{linear}	0.67	3.0	0.7	0.67	3.0	0.7	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3	0.29	1.4	1.4
CJ_{linear} and $CA_{\text{hyperbolic}}$	0.50	2.0	1.0	0.50	2.0	1.0	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3
CJ_{linear} and $CA_{\text{exponential}}$	0.67	3.0	0.7	0.67	3.0	0.7	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.29	1.4	1.3	0.29	1.4	1.3	0.25	1.3	1.3
$CJ_{\text{hyperbolic}}$ and CA_{linear}	0.67	3.0	0.7	0.67	3.0	0.7	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3
$CJ_{\text{hyperbolic}}$ and $CA_{\text{hyperbolic}}$	0.50	2.0	1.0	0.50	2.0	1.0	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.33	1.5	1.3
$CJ_{\text{hyperbolic}}$ and $CA_{\text{exponential}}$	0.67	3.0	0.7	0.67	3.0	0.7	0.40	1.7	1.2	0.40	1.7	1.2	0.40	1.7	1.2	0.33	1.5	1.3	0.33	1.5	1.3	0.33	1.5	1.3

Note: The eight scenarios from alternative (2) in which a gradient in clutch size builds up are shown (see Table 1). The ratio $K_{\text{Summer}}/K_{\text{Winter}}$ models the amount of seasonality of resources; 1.01 corresponds to the tropics and 1.35 to Baden-Württemberg, Germany. It should be noted that column $K_{\text{Summer}}/K_{\text{Winter}} = 1000/1000 = 1.00$ means no seasonality of resources together with a cost of reproduction (alternative 3).

seasonality of resources is present (alternative 1), the genotype with the highest clutch size always prevails and consequently no gradient was observed. The latter observations suggest that Ashmole's (1963) hypothesis works only if there are costs of reproduction, which is a general assumption of evolutionary life-history theory to counteract infinite reproductive rates (Law, 1979). Although Ashmole (1963) did not take into consideration cost of reproduction, he identified one important ecological mechanism that is required to explain latitudinal variation in clutch size: populations are strongly limited by resources during the non-breeding season and clutch size is determined by resources available during the breeding season relative to the non-breeding season. In the simulation experiments where no seasonality of resources was assumed (alternatives 3 and 4), no gradient was observed independent of whether trade-offs of reproduction had been assumed or not. The latter results suggest that potential differences in the resource level during the breeding season between the temperate regions and the tropics cannot account for the latitudinal gradient in clutch size.

Validity of cost scenarios

At least two of the eight scenarios where a latitudinal gradient in clutch size builds up under alternative (2) seem to be realistic for natural bird populations. For different bird species, brood-manipulation experiments have demonstrated that nestling survival decreases hyperbola-like with the number of eggs in a nest (Lack, 1948) and that annual adult survival decreases hyperbola-like with increasing numbers of young fledged (Dijkstra *et al.*, 1990). Moreover, for some species, a trade-off between clutch size and offspring survival was demonstrated, but none was found for survival and fecundity of adults (Pettifor, 1993a,b). For other species, both juveniles and adults were negatively affected by an increased brood size (Dijkstra *et al.*, 1990). These experiments suggest that at least cost scenarios ($CJ_{\text{hyperbolic}}$ and $\neg CA$) and ($CJ_{\text{hyperbolic}}$ and $CA_{\text{hyperbolic}}$) are relevant for birds. Nevertheless, our simulation results for alternative (2) demonstrate that linear or hyperbolic costs for juveniles are sufficient to explain the clutch size gradient. In this situation, additional costs for parents modify only the slope of this gradient (Table 2) and therefore are of minor importance for this pattern. If costs affect only parents no gradient builds up, suggesting that costs for offspring are indispensable for the gradient. The result that costs of reproduction that act on adults, but not on juveniles, are insufficient to generate a latitudinal gradient in clutch size was also obtained with the more complex model (not presented here) that allows for cost of reproduction in summer and in winter for both life-stages. Thus, this additional finding does corroborate the generality of our conclusion derived from the simpler model presented here.

For the tropics and the temperate region, we assumed equal cost functions but cost functions may differ between the regions. For example, tropical birds have extended parental care (Martin, 1996; Russell, 2000; Schaefer *et al.*, in press), which may result in different cost functions. Our simulation study shows that the tropical clutch size ($K_{\text{Summer}}/K_{\text{Winter}} = 1.01$; Table 2) varies by at most one egg dependent on the different cost functions assumed for juveniles and adults. Similarly, the assumption of different cost functions for juveniles or adults altered the clutch size predicted at a specific latitude by at most one egg in the temperate region ($K_{\text{Summer}}/K_{\text{Winter}} > 1.01$; Table 2). These observations suggest that clutch sizes predicted at specific latitudes are relatively robust against cost functions assumed.

Clutch size as a function of latitude

The linear-like increase in clutch size observed in the eight scenarios out of 15 for the second alternative (Table 2) corresponds to field observations and, therefore, clutch sizes predicted by our model are overall realistic at least for single-brooded birds. In cost scenarios ($CJ_{\text{hyperbolic}}$ and CA_{linear}) and ($CJ_{\text{hyperbolic}}$ and $CA_{\text{exponential}}$), our model predicts a clutch size of one for the tropics and three and four, respectively, at latitude 50° ($K_{\text{Summer}}/K_{\text{Winter}} \approx 1.33$), which is consistent with Moreau's (1944) observations on the owl genus *Strix*. In contrast, clutch sizes predicted for cost scenario (CJ_{linear} and $\neg CA$) comply with Lack's (1968) and Brown and Lomolino's (1998) observations for the owl family *Strigidae*. For cost scenario ($CJ_{\text{hyperbolic}}$ and $\neg CA$), the model predicts three eggs in the tropics and four eggs in the temperate region, which coincides with Moreau's (1944) data on the family *Falconidae*, in particular with the clutch size of the European Kestrel *Falco tinnunculus* (Van Zyl, 1999) and with the clutch sizes in the family *Accipitridae* (Moreau, 1944).

Life-table variables and correlations

Although there are some converse observations (Karr *et al.*, 1990), it is widely accepted that annual adult survival rates of birds decrease away from the equator (Johnston *et al.*, 1997; Ricklefs, 1997), that annual fecundity (number of offspring per year and adult) is inversely proportional to annual adult survival (Ricklefs, 1997) and that the mean life expectancy of tropical birds is higher than that of their temperate counterparts (Peach *et al.*, 2001).

For the eight scenarios out of 15 in which we obtained a gradient in clutch size, these differences and correlations among life-table variables of tropical, subtropical and temperate avian species were reproduced by our model for single-brooded species. The annual survival rate of the European kestrel shows a decrease with increasing latitude. For the temperate region, our model predicts an adult survival rate between 0.29 and 0.40 [$K_{\text{Summer}}/K_{\text{Winter}} \approx 1.33$ (1.45) corresponds to a latitude of about 50° (60°), Table 3]. This rate is lower than that found for the European kestrel in Switzerland (0.65; Schifferli, 1964), The Netherlands (0.58; Cavé, 1968) and Finland (0.56; Nordstrom, 1963). In different temperate regions, annual adult survival rates of several raptors have been shown to range from 0.43 to 0.82 (Newton, 1979), and are thus again somewhat higher than those obtained in our model. Mean life expectancy of the European kestrel and the common buzzard (*Buteo buteo*) show a decrease with increasing latitude. For the European kestrel, the mean life expectancy is 1.3 years in Finland (Nordstrom, 1963) and 1.5 years in The Netherlands and Switzerland (Schifferli, 1964; Cavé, 1968). For the common buzzard, expectancy is 1.3 years in Fennoscandia (Olsson, 1958) and 1.5 years in Germany (Mebs, 1964). These expectancies conform to our model's predictions, ranging between 1.4 and 1.7 for the temperate region (Table 3). The fecundities of temperate and pooled tropical and subtropical raptor species show an increase with increasing latitude (Newton, 1979), and are thus inversely proportional to adult survival that shows a decrease with increasing latitude. The fecundities of these temperate raptors range from 0.4 to 2.8 (mean = 1.262; Newton, 1979), whereas those of tropical and subtropical species range between 0.4 and 0.8 (mean = 0.516; Newton, 1979). Mean fecundities observed in the field thus lie around the values predicted by our model (tropics: 0.7–1.2; temperate region: 1.2–1.4; Table 3).

In conclusion, data on at least two raptor species support the widely assumed latitudinal differences in relationships in life-table variables. These are reproduced by our model in eight scenarios out of the 15 where a latitudinal gradient in clutch size builds up.

Applicability of the model to multi-brooded birds

Although our model assumes single-brooded birds, the clutch sizes predicted are also in a realistic range for multi-brooded tropical and temperate birds (Moreau, 1944; Lack, 1968; Cody, 1971; Ricklefs, 1980; Brown and Lomolino, 1998). Differences and correlations among life-table variables of tropical and temperate species that were mainly derived for Passeriformes but are also valid for some raptors hold also in our model. This suggests that these are general patterns in birds that are reproduced in our model. More evidence for the generality of our results comes from further simulation studies (not presented here). These show that the results derived for single-brooded birds are still valid if we assume an equal number of broods greater than one (we tested two and three broods per generation) for tropical and temperate species and that juvenile survival is independent of nesting time. For all scenarios studied here, predicted clutch sizes did not differ from those calculated by the single-brooded model and did not depend on the number of broods, per breeding season. If we assumed multiple broods, juvenile survival was lower than in the single-brooded model presented here. In particular, for the eight scenarios out of the 15 tested, these additional simulations suggest (i) that clutch sizes predicted by the single-brooded model may be valid for tropical and temperate birds that have multiple broods, and (ii) that the number of broods that may possibly differ between the regions may not affect the optimal clutch size at a specific latitude.

Predictions for clutch size evolution in seasonal environments

Our results conform to a wide range of geographic clutch size variation that might be attributed to the evolution of this life-history trait in a seasonal environment. In addition to the latitudinal gradient in clutch size, they also account for longitudinal variation in avian clutch size. Birds lay larger clutches in eastern than in western Europe (Lack, 1954; Bell, 1996), reflecting higher levels of seasonal variation in eastern than in western Europe (Lemoine and Böhning-Gaese, 2003).

Differences in clutch size and fecundity of temperate resident and migratory birds (Böhning-Gaese *et al.*, 2000) conform also to predictions under alternative (2). Migration of temperate birds might be interpreted as a behaviour that reduces the degree of seasonal variation in resources for migrants in comparison to temperate residents. Under the assumption that migration costs are not too high, birds that migrate to the warmer southern region suffer from lower winter mortality than the residents overwintering in the colder temperate region. From alternative (2), we would expect that migratory birds have a lower clutch size and a lower annual fecundity than temperate residents, which has been shown for North American and European land birds (Böhning-Gaese *et al.*, 2000). Resources available on the wintering grounds, however, are reduced by the influx of temperate migrants, leading to higher winter mortality among southern residents. From our model, we predict that clutch size of southern resident birds increases with the proportion of temperate migrants overwintering in their habitats, which has been demonstrated recently by Yom-Tov and Geffen (2002).

Finally, the results obtained under alternative (2) allow us to predict the influence of climate change on avian clutch size. There is good evidence that due to global warming winter temperatures will increase more than summer temperatures in Europe (Hurrell, 1995; Vygodskaya *et al.*, 1995). This will result in lower winter mortalities for European birds than currently observed and a lower seasonality of resources for resident species. From our results, we would expect a decrease in clutch size for resident species that has already been demonstrated at the continental scale by Sanz (2003) for pied flycatchers (*Ficedula hypoleuca*) and at the regional scale for the blackcap (*Sylvia atricapilla*; F. Pulido, personal communication).

CONCLUSIONS

Our simulation study demonstrates that Ashmole's hypothesis is able to explain the latitudinal gradient in clutch size by seasonality of resources if, additionally, individuals experience a cost of reproduction. From our simulation results for alternative (2), we know that linear or hyperbolic costs for juveniles are sufficient to explain the clutch size gradient. In this situation, additional costs for parents modify only the slope of this gradient (Table 2) and therefore are of minor importance. If costs affect only parents no gradient builds up, suggesting that costs for offspring are indispensable for a gradient. Since Hurlbert and Haskell (2003) have recently found that summer production exhibits no gradient with latitude whereas winter production is lower and shows a decrease with increasing latitude, Ashmole's assumption of seasonality in food availability resulting in winter mortality should be unquestioned. Consequently, the final validation of Ashmole's hypothesis relies heavily on the demonstration of a cost of reproduction in the field, as required by life-history theory (Law, 1979). This result should encourage ornithologists to demonstrate experimentally and describe mathematically trade-offs for reproduction, especially those acting on offspring.

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