Seasonal Sex Ratio Trend in the European Kestrel: An Evolutionarily Stable Strategy Analysis

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ABSTRACT: We present an evolutionarily stable strategy (ESS) model to analyze selection on seasonal variation in the brood sex ratio, as observed in several species of raptorial birds. The model is specifically tailored to the life history of the European kestrel, and it reflects the maturation time hypothesis, the idea that a seasonal sex ratio trend has evolved because of sex differences in the dependence of age of first breeding on date of birth. First we show how to derive a fitness function in the context of a seasonal environment. Model parameters are estimated from field data in order to derive quantitative predictions. Since little is known about constraints on sex ratio control in birds, we analyze three scenarios, each corresponding to a different strategy set. We consider a model without constraints on sex ratio control, a model where the sex ratio trend is constrained to be linear, and a mechanistic model incorporating a plausible mechanism of sex ratio control in birds. One of the models yields an ESS sex ratio trend that closely resembles the trend observed in the field. However, the predictions are very sensitive to the choice of strategy set. Moreover, the selective forces generated by sex differences in maturation are rather weak. In fact, the mechanistic model shows that seemingly negligible costs of sex ratio control may be sufficient to overcome the adaptive value of adjusting the sex ratio.

Keywords: brood sex ratio, age at maturity, seasonality, evolutionary stability, life history.

The average brood sex ratio (proportion sons) of birds, when measured at the population level, is typically very close to 0.5, and the few reports of significant departures from parity concern deviations that are relatively small in magnitude (reviews in Clutton-Brock 1986; Gowaty 1990, 1993). This might be interpreted as prima facie evidence

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that the mechanism of chromosomal sex determination is too rigid to allow birds to adaptively adjust the sex ratio of their brood. However, while deviations from parity at the population level seem rare, recent studies show that there is systematic sex ratio variation within populations of birds (e.g., Ellegren et al. 1996; Lessells et al. 1996). The most striking example of such facultative sex ratio adjustment has been found in the Seychelles warbler *Acrocephalus sechellensis* (Komdeur et al. 1997), where the sex ratio varies consistently from one extreme to the other, overturning the notion that birds cannot adjust the sex ratio at birth. Another interesting example of facultative sex ratio adjustment in birds occurs in several species of raptors, where the brood sex ratio changes systematically in the course of the breeding season (Dijkstra et al. 1990; Olsen and Cockburn 1991; Daan et al. 1996). Intriguingly, despite close phylogenetic relatedness, similar ecology, and comparable sexual size dimorphism, the directions of these seasonal sex ratio trends differ between species. Some species (European kestrel and lesser kestrel) show a negative trend; that is, they produce an excess of sons early in the season and an excess of daughters later in the season. Other species (sparrowhawk, goshawk, marsh harrier, peregrine falcon) show the opposite trend, with an overproduction of daughters early in the season and sons late in the season. By means of a population genetical simulation model, Daan et al. (1996) showed that, qualitatively, these differences might be caused by sex- and species-specific differences in the relationship between birth date and maturation time (the maturation time hypothesis). Here we investigate the merit of this hypothesis with an analytical evolutionarily stable strategy (ESS) approach.

An ESS analysis is performed in three steps (e.g., Parker and Maynard Smith 1990). First, a strategy set is defined with respect to the trait of interest. This set comprises a description of the traits that are phenotypically feasible, and as such, it reflects constraints within which adaptive evolution is thought to take place. Second, a fitness function is required, which relates the "adaptedness" of a phenotypic trait in the strategy set to characteristics of the population and/or the environment. Third, an ESS crite-

rion is used to characterize those resident strategies that are evolutionarily stable in that they are immune to invasion attempts of rare mutants.

This recipe may seem quite straightforward, but in the application to real-world problems a number of difficulties arise. First, the choice of strategy set and the implementation of constraints are often rather ad hoc. In fact, the necessary detailed knowledge of which options are feasible and which are not is nearly always lacking. Second, in a life-history context, the fitness concept is not straightforward but has to be based on population dynamical considerations. Third, the ESS approach is based on the idea that evolution proceeds via a sequence of temporally uncoupled gene-substitution events. It is not clear yet to what extent this simplified picture of evolution captures the essence of evolution in polymorphic real populations.

In this article, we apply the ESS approach to a life-history model specifically tailored to the European kestrel. We show how to derive a fitness function that can be used in the context of a seasonal environment. We use life-history parameters estimated from field data to derive quantitative predictions for the evolutionarily stable seasonal sex ratio trend to be expected on the basis of our model. Because knowledge of constraints operating on sex allocation in birds is essentially lacking, we consider a number of different strategy sets. This allows us to judge the robustness of the predictions with respect to structural features of the model. In particular, we investigate a mechanistic model in order to assess the selective consequences of a costly mechanism of sex ratio control.

An Overview of the Method

We summarize here the basic ESS approach in a life-history context (see Taylor 1996). Consider a monomorphic population in which all individuals exhibit the same phenotypic trait (or strategy) s^*. Suppose the population is subdivided into a number of discrete "stages" (e.g., females, subadult males, adult males). Let n_i^* denote the number of individuals in stage i. The number of individuals in stage i in the next season is then given by

$$n_i^{*\prime} = \sum_j a_{ij} n_j^*,\qquad(1)$$

where a_{ij} is the average number of individuals of stage i contributed to the next time unit or season by one individual of stage j (e.g., Caswell 1989). These contributions should be weighed according to genetic representation. For example, in a diploid sexual population, offspring typically carry half a parent's genes, and contribution of offspring should then be multiplied by 1/2. More compactly, equation (1) may be written as

$$\boldsymbol{n}^{*\prime} = \mathbf{A}(s^*)\boldsymbol{n}^*.\qquad(2)$$

The notation indicates that the stage transition matrix $\mathbf{A}$ depends on the phenotypic parameter s^*. Under some mild conditions, the stage distribution $\boldsymbol{n}^*$ will converge to a stable stage distribution $\boldsymbol{u}^*$, and the population will grow at a rate λ^* given by the dominant eigenvalue of $\mathbf{A}$.

Let us assume that the resident phenotype s^* is induced by an allele a^* at some autosomal locus. Suppose a rare allele a enters the population that, in heterozygous condition, induces the mutant phenotype s. As long as the population is dominated by homozygous residents, it is reasonable to assume that mutants only mate with residents. Homozygous aa individuals can be neglected since they are extremely rare. Let there be n_i mutant individuals in stage i. The growth dynamics of the mutant subpopulation is of the form

$$n_i' = \sum_j b_{ij} n_j,\qquad(3)$$

where the stage transition matrix $\mathbf{B} = (b_{ij})$ depends not only on the mutant phenotype s but also on the resident phenotype s^*. Hence, in short,

$$\boldsymbol{n}' = \mathbf{B}(s, s^*)\boldsymbol{n}.\qquad(4)$$

The asymptotic growth rate of the mutant subpopulation is given by the dominant eigenvalue $\lambda = \lambda(s, s^*)$ of the matrix $\mathbf{B} = \mathbf{B}(s, s^*)$. Clearly, $\mathbf{B}(s^*, s^*) = \mathbf{A}(s^*)$ and $\lambda(s^*, s^*) = \lambda^*$; that is, a mutant phenotypically indistinguishable from the resident must have the same per capita growth rate as the resident. The mutant phenotype will spread if it has a higher per capita growth rate than the resident ($\lambda > \lambda^*$). Otherwise ($\lambda < \lambda^*$) it will be driven to extinction.

As a consequence, a necessary condition for evolutionary stability of resident strategy s^* against all invasion attempts by rare mutant strategies $s \neq s^*$ is given by

$$\lambda(s, s^*) \leq \lambda(s^*, s^*).\qquad(5)$$

Thus, $\lambda(s, s^*)$ may be viewed as a fitness function for a rare mutant strategy s in a monomorphic population with resident strategy s^*. ESS values of s^* may then be found by maximizing $\lambda(s, s^*)$ with respect to the mutant behavior s. In practice, it is often the case that the mutant phenotype is expressed in only one stage of the life history, say, in stage 1. In that case, one does not need to maximize the population parameter $\lambda(s, s^*)$. Instead, as we show in appendix A, one may equivalently but more conveniently maximize the reproductive value v_1 of individuals in stage 1:

Table 1: Seasonal dependence of life-history parameters of the kestrel in the Netherlands (see Dijkstra 1988; Daan et al. 1996) and the observed brood sex ratio (proportion sons)

	Part of breeding season				Regression	R^2
	1	2	3	4		
Standardized date (t)	$-3/8$	$-1/8$	$1/8$	$3/8$		
Clutch size	5.91	5.49	5.13	4.64	$5.29 - 1.67t$	.997
Survival to age 1 yr	.273	.169	.175	.115	$.18 - .20t$	.843
Recruitment (F)	1.61	.928	.898	.534	$\mathbf{.99 - 1.31}t$	.877
Male 1-yr breeding probability (α)	.65	.74	.61	.53	$\mathbf{.63 - .20}t$	.525
Brood sex ratio (σ)	.536	.517	.515	.457	$.51 - .10t$	.815
SE (mean σ)	.016	.018	.017	.029		
Adult survival (P)					**.7**	

Note: Numerical values that appear in bold were used as parameter values in the ESS model.

$$v_1(s, s^*) = \frac{1}{\lambda^*} \sum_i v_i^* b_{i1}(s, s^*), \qquad (6)$$

where $v_i^* = v_i(s^*, s^*)$ denotes the reproductive value of resident individuals in stage i, and λ^* is the growth rate of the resident population. The interpretation of equation (6) is quite transparent: $b_{i1}(s, s^*)$ is the contribution of a mutant individual in stage 1 to stage i in the next season, and the fitness consequence of this contribution is represented by the reproductive value v_i^* of individuals in stage i, discounted by the per-season population growth rate λ^*.

Life History of the Kestrel

To set the stage for a population dynamical model tailored to the kestrel, we first give an (idealized) account of the kestrel's life history. This description is based on a well-studied population in the Netherlands (see Dijkstra 1988; Daan et al. 1996), the same population in which a seasonal sex ratio trend was found (Dijkstra et al. 1990).

Females

Although kestrels have overlapping generations, their life history is relatively simple. This is especially true for females, who have no real age structure in their demographic traits: nearly all females start breeding when they are 1 yr old, and from this age onward, their yearly survival and reproductive output are independent of age. A much more important determinant of a female's reproductive success is timing of breeding within the season. As in many birds with single broods per year (Klomp 1970), clutch size and first year survival in the kestrel decrease systematically throughout the season (e.g., Cavé 1968; Dijkstra 1988). Recruitment (=clutch size × first-year survival) declines

approximately linearly with laying date t, say, according to

$$F(t) = r_0 - r_1 t. \qquad (7)$$

The estimates of r_0 and r_1 for the kestrel population in the Netherlands are given in table 1.

If breeding is uniformly distributed, the average recruitment rate is obtained by integrating over the standardized season $S = [-1/2, 1/2]$:

$$\bar{F} = \int_S F(t)dt = r_0. \qquad (8)$$

Since in birds females are the heterogametic sex, we assume that the brood sex ratio $\sigma(t)$ (proportion sons) as a function of time t in the season is under maternal control. The average sex ratio among recruits is then given by

$$\bar{\sigma} = \frac{1}{\bar{F}} \int_S F(t)\sigma(t)dt. \qquad (9)$$

A female's probability of survival from one season to the next is independent of the timing of breeding and is denoted by P (empirical estimate in table 1).

Males

The life history of male kestrels differs in one important aspect from that of females. Only some males (say, a fraction $\alpha(t)$) manage to start breeding when they are 1 yr old, depending on their date of birth (t) (we use the terms "laying date" and "birth date" interchangeably). Nearly all other males start breeding when they are 2 yr old. The

probability that a son starts breeding as a yearling, henceforth called "maturation rate," depends in an approximately linear fashion on laying date:

$$\alpha(t) = a_0 - a_1 t. \tag{10}$$

Regression estimates of a_0 and a_1 for Dutch kestrels can be found in table 1.

Averaged over the season, the mean maturation rate is given by

$$\overline{\alpha} = \frac{1}{\overline{F}\overline{\sigma}} \int_S F(t)\sigma(t)\alpha(t)\,dt. \tag{11}$$

Note that the average maturation rate depends on the seasonal sex ratio trend as specified by $\sigma(t)$. The average reproductive output of males may differ from that of females. In fact, if $\overline{F}$ is the average recruitment of a female, then the average recruitment of a male is given by $R\overline{F}$, where

$$R = \frac{\text{number of breeding females}}{\text{number of breeding males}}, \tag{12}$$

the inverse of the operational sex ratio. Male survival to the next season does not differ from female survival and is also denoted by P (see table 1).

Population Dynamics

On the basis of the above, a kestrel population in the breeding season may be decomposed into three life-history stages: females, nonbreeding 1-yr-old males, and breeding males. Suppose such a population, monomorphic for a seasonal sex ratio trend $\sigma^*(t)$, is invaded by a rare mutant allele inducing female carriers to produce a sex ratio trend $\sigma(t)$. Let the vector $\boldsymbol{n} = (n_1, n_2, n_3)$ keep track of the numbers of mutants among, respectively, females, nonbreeding males, and breeding males. The change of these numbers from one season to the next is described by the matrix

$$\mathbf{B}(\sigma, \sigma^*) = \begin{pmatrix} P + \frac{1}{2}(1-\overline{\sigma})\overline{F} & 0 & \frac{1}{2}(1-\overline{\sigma}^*)\overline{F}R^* \\ \frac{1}{2}(1-\overline{\alpha})\overline{\sigma F} & 0 & \frac{1}{2}(1-\overline{\alpha}^*)\overline{\sigma}^*\overline{F}R^* \\ \frac{1}{2}\overline{\alpha\sigma F} & P & P + \frac{1}{2}\overline{\alpha}^*\overline{\sigma}^*\overline{F}R^* \end{pmatrix}. \tag{13}$$

The three stages of mutants and the dynamic transitions between them can be visualized as depicted in figure 1. The factor 1/2 in front of terms involving reproduction
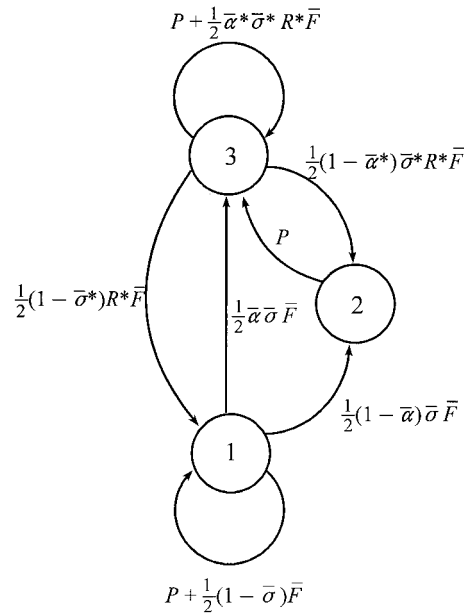

Figure 1: Life-cycle graph for kestrels with the mutant strategy σ in a resident population with strategy σ^*. The stages 1, 2, and 3 represent, respectively, females, nonbreeding yearling males, and breeding males. Arrows symbolize the per capita contributions to the different stages in the next season. The factor 1/2 reflects the degree of relatedness of parents to their offspring.

reflects the degree of relatedness of parents to their offspring. The relative fertility of mutant males is given by the ratio R^* of females to breeding males in the resident population. Notice that offspring of mutant males are produced according to the resident phenotype, since mutant males effectively only mate with resident females who are assumed to be in control of the sex ratio.

We have included seasonality in the model by taking into account the effect of a seasonal sex ratio trend $\sigma(t)$ on the average sex ratio $\overline{\sigma}$ among recruits and the average male maturation rate $\overline{\alpha}$. We should caution at this point that this approach is only correct as long as there is no correlation between the laying dates of parents and offspring, an assumption that seems to be corroborated by empirical evidence in the kestrel (C. Dijkstra, personal communication).

By setting $\sigma(t) = \sigma^*(t)$, the stage transition matrix $\mathbf{B}^* = \mathbf{B}(\sigma^*, \sigma^*)$ represents the dynamics of the resident population. It may seem that the factor $R^* = n_1^*/n_3^*$ in $\mathbf{B}^*$'s elements makes the resident population dynamics (eq. [2]) nonlinear, but actually this is not the case because R^* cancels out of equation (2) and $\mathbf{B}^*$ reduces to lower triangular form. It is then straightforward to verify that the growth rate of this population, which equals the dominant eigenvalue of $\mathbf{B}^*$, is given by

$$\lambda^* = P + (1 - \overline{\sigma}^*)\overline{F}. \tag{14}$$

The ratio of breeding females to males in the resident population can be found from the stable stage distribution u^*. Technically, u^* is given by the dominant right eigenvector of $\mathbf{B}^*$. The result is

$$R^* = \frac{u_1^*}{u_3^*} = \left(\frac{1 - \overline{\sigma}^*}{\overline{\sigma}^*}\right)\frac{P + (1 - \overline{\sigma}^*)\overline{F}}{P + \overline{\alpha}^*(1 - \overline{\sigma}^*)\overline{F}}. \tag{15}$$

Up to a constant of proportionality, the average reproductive values of the three stages in the resident population are given by

$$v_1^* = 1,$$

$$v_2^* = \frac{R^*P}{\lambda^*}, \tag{16}$$

$$v_3^* = R^*.$$

These are just the elements of a dominant left eigenvector of $\mathbf{B}^*$.

Now we can write down the reproductive value of a mutant female with sex ratio trend $\sigma(t)$ in a resident population with sex ratio trend $\sigma^*(t)$:

$$v_1(\sigma, \sigma^*) = \frac{1}{\lambda^*}(v_1^* b_{11} + v_2^* b_{21} + v_3^* b_{31}). \tag{17}$$

By inserting the appropriate elements of equations (13), (14), and (16) and by removing all terms that do not contain the mutant strategy $\sigma(t)$, we get the simplified expression

$$v_1(\sigma, \sigma^*) \cong \overline{\sigma}\left[\frac{1 - \overline{\sigma}^*}{\overline{\sigma}^*}\frac{P + \overline{\alpha}(1 - \overline{\sigma}^*)\overline{F}}{P + \overline{\alpha}^*(1 - \overline{\sigma}^*)\overline{F}} - 1\right]. \tag{18}$$

At an ESS σ^*, $v_1(\sigma, \sigma^*)$ is maximized with respect to the mutant strategy σ. We shall consider cases where the strategies $\sigma = \sigma(t)$ are characterized by a finite number of parameters, say $x = (x_1, ..., x_k)$, where the x_i's correspond to the switch point of a bang-bang strategy or to the slope or intercept of a linear sex ratio trend. Therefore, the reproductive value of a mutant female may be viewed as a function $v_1(x, x^*)$, and the ESS is found by solving

$$\frac{\partial v_1}{\partial x}\bigg|_{x=x^*} = 0 \quad \text{and} \quad \frac{\partial^2 v_1}{\partial x^2}\bigg|_{x=x^*} < 0. \tag{19}$$

In our case, the selection differential $\partial v_1/\partial x$ can be de-

composed into two terms, one representing the effect of the strategic parameters on the mean sex ratio $\overline{\sigma} = \overline{\sigma}(x)$, the other representing the effect of x on the mean male maturation rate $\overline{\alpha} = \overline{\alpha}(x)$. In fact, differentiation of equation (18) yields

$$\frac{\partial v_1}{\partial x}\bigg|_{x=x^*} = \frac{1 - 2\overline{\sigma}^*}{\overline{\sigma}^*}\frac{\partial\overline{\sigma}}{\partial x}\bigg|_{x=x^*}$$

$$+ \frac{(1 - \overline{\sigma}^*)^2\overline{F}}{P + \overline{\alpha}^*(1 - \overline{\sigma}^*)\overline{F}}\frac{\partial\overline{\alpha}}{\partial x}\bigg|_{x=x^*}. \tag{20}$$

The first term on the right-hand side represents the direction of selection due to changes in the average sex ratio caused by variation in x. Clearly, if the population sex ratio in the resident population is male biased (i.e., $\overline{\sigma}^* > 1/2$), then this selection differential is negative if a change in x leads to an even more male-biased sex ratio, whereas it is positive if a change in x leads to a more female-biased sex ratio. The second term on the right-hand side of equation (20) represents the selection differential due to changes in the male maturation rate as a result of changes in x. This selection differential is always positive as long as a change in x causes a faster maturation rate.

ESS without Constraints

If there are no constraints on sex ratio control, then the optimal strategy is a bang-bang strategy: produce only sons in the beginning of the season, up to a point after which only daughters should be produced. It is easy to see why this strategy is optimal. Consider any sex ratio trend σ^* that is not a bang-bang strategy. There exists a unique bang-bang strategy σ_b, yielding the same average population sex ratio $\overline{\sigma}_b = \overline{\sigma}^*$, and it is obvious that σ_b induces a faster mean male maturation rate $\overline{\alpha}_b = \overline{\alpha}^*$. Therefore, by (20), this bang-bang strategy always invades.

The strategy set of a bang-bang strategy is characterized by the switch-point $\tau \epsilon S = [-1/2, 1/2]$, the time of the season after which only daughters are produced. From equations (9) and (11) we calculate

$$\frac{\partial\overline{\sigma}}{\partial\tau}\bigg|_{\tau=\tau^*} = \frac{F(\tau^*)}{\overline{F}}$$

$$\frac{\partial\overline{\alpha}}{\partial\tau}\bigg|_{\tau=\tau^*} = \frac{F(\tau^*)}{\overline{\sigma}^*\overline{F}}[\alpha(\tau^*) - \overline{\alpha}]. \tag{21}$$

Inserting this in (20) and equating to 0 yields the following necessary condition for an ESS:

$$\left.\frac{\partial v_1}{\partial \tau}\right|_{\tau=\tau^*} \propto (1 - 2\overline{\sigma}^*) + \frac{[\alpha(\tau^*) - \overline{\alpha}^*](1 - \overline{\sigma}^*)\overline{F}}{P + \overline{\alpha}^*(1 - \overline{\sigma}^*)\overline{F}} = 0. \quad (22)$$

Since $\alpha(t)$ is decreasing, the second term on the right-hand side is always negative. Therefore, the first term on the right-hand side must be positive, which implies that in an ESS the average population sex ratio must be female biased ($\overline{\sigma}^* < 1/2$).

When we substitute equations (7) and (10) for $F(t)$ and $\alpha(t)$, respectively, solving (22) amounts to finding the roots of a third-order polynomial in τ^*. Inserting the values of r_0, r_1, a_0, a_1, and P, as given in table 1, we obtain the following result.

Result 1. For the Dutch kestrel population, the optimal seasonal sex ratio trend is a bang-bang strategy, switching from producing all-son broods to producing all-daughter broods at time $\tau^* = -0.154$ (i.e., after 34.6% of the season has passed). The resulting average population sex ratio is slightly female biased and given by $\overline{\sigma}^* = 0.496$.

ESS Linear Sex Ratio Trends

The seasonal sex ratio trends observed in raptors (Daan et al. 1996) are clearly not in line with a bang-bang strategy. In fact, they are all approximately linear. One might then formulate the following question. Suppose seasonal sex ratio trends are constrained to be linear for some unknown reason. What would then be the evolutionarily stable trend? Given our lack of knowledge about the constraints operating in reality, this is the most parsimonious assumption. Of course, the model cannot explain why the observed trends are linear but only which of the linear trends is evolutionarily stable.

Let us suppose a linear sex ratio trend over the season $S = [-1/2, 1/2]$ is characterized by $\beta = (\beta_0, \beta_1)$. The intercept β_0 corresponds to the sex ratio at midseason ($t = 0$), and β_1 corresponds to the slope of the sex ratio trend. The strategy set used by Daan et al. (1996) in their simulation model is a special case of this, with $\beta_0 = 1/2$. Because of the obvious constraint $0 \leq \sigma(t) \leq 1$, the sex ratio trend is actually piecewise linear when β_0 and β_1 are too large or too small:

$$\sigma(t) = \begin{cases} 1 & \text{if } \beta_0 + \beta_1 t \geq 1 \\ \beta_0 + \beta_1 t & \text{if } 0 < \beta_0 + \beta_1 t < 1 \,. \\ 0 & \text{if } \beta_0 + \beta_1 t \leq 0 \end{cases} \quad (23)$$

For extreme values of β_0 and β_1, $\sigma(t)$ approaches a bang-bang strategy. Again, by calculating the average sex ratio (eq. [9]) among recruits and the average male maturation rate (eq. [11]), and inserting the resulting expressions in (18), one obtains the reproductive value $v_1(\beta_0, \beta_1)$ of a mutant female with strategy β in a resident population with strategy β^*. An ESS, if it exists, can be found by investigating the selection differential (eq. [20]).

ESS Intercept

First, we calculated the ESS intercept β_0^* of a linear sex ratio, given a fixed slope β_1. The analytical formulas are not very enlightening, so we refrain from showing them here. For the parameters in table 1, the result is shown in figure 2. An interesting special case is obtained for $\beta_1 = 0$. This corresponds to the situation in which a female is not able to adjust the sex ratio of her brood to the laying date, but she can influence the average sex ratio which for $\beta_1 = 0$ equals $\overline{\sigma} = \beta_0$. It is easy to calculate from (11) that $\overline{\alpha} = a_0 - a_1 r_0/(12r_1)$, independent of β_0. The selection differential (eq. [20]) reduces to
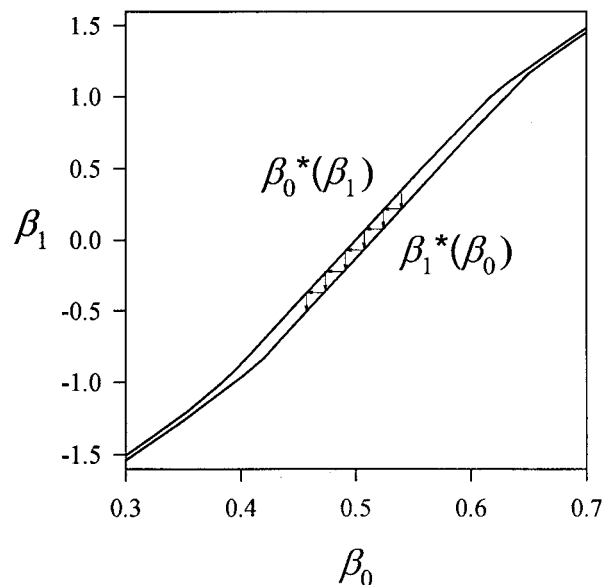

Figure 2: Curves corresponding to the ESS intercept $\beta_0^*(\beta_1)$ given a slope β_1 and to the ESS slope $\beta_1^*(\beta_0)$ given an intercept β_0. The kinks occur where the sex ratio trends become piecewise linear rather than linear. Since the curves do not cross, an overall ESS $\beta^* = (\beta_0^*, \beta_1^*)$ does not exist. The arrows indicate the direction of selection, suggesting that β_0^* and β_1^* should evolve to ever lower values.

$$\left.\frac{\partial v_1}{\partial \beta_0}\right|_{\beta_0=\beta_0^*} = \frac{1-2\beta_0^*}{\beta_0^*}\begin{cases} <0 & \text{iff } \beta_0^* > 1/2 \\ =0 & \text{iff } \beta_0^* = 1/2 \,. \\ >0 & \text{iff } \beta_0^* < 1/2 \end{cases} \quad (24)$$

Hence, if the resident average sex ratio is female biased ($\beta_0^* < 1/2$), any mutant $\beta_0 > \beta_0^*$ can successfully invade, and, conversely, if the resident average sex ratio is male biased ($\beta_0^* > 1/2$), any mutant $\beta_0 < \beta_0^*$ has higher fitness. Therefore, we obtain the following result.

Result 2. If selection only acts on the average brood sex ratio, an even sex ratio is the unique ESS.

ESS Slope

Next we calculated the ESS slope β_1^*, given an intercept β_0. For the parameters in table 1, the result is shown in figure 2. We focus on one special case where the sex ratio at midseason is fixed at parity (i.e., $\beta_0 = 1/2$). This constraint is somewhat arbitrary (alternatively, we could have used the constraint $\overline{\sigma} = 1/2$), but it corresponds precisely to the strategy set used in the simulation model of Daan et al. (1996), and we want to compare our analytical results to their simulation results. By equating (20) with 0, one obtains a quadratic equation in β_1^*. Since the analytic solutions inspire little insight, we present numerical solutions only. For the parameter estimates in table 1, we obtain the following result.

Result 3. For the Dutch kestrel population, the evolutionarily stable linear sex ratio trend with a fixed even sex ratio at midseason has the slope $\beta_1^* = -0.13$. That is, the proportion of sons is expected to decrease by 0.13 in the course of the breeding season. The average population sex ratio is male biased and given by $\overline{\sigma} = 0.514$.

The result is illustrated in figure 3, where three seasonal sex ratio trends are depicted: the empirical trend of the Dutch kestrel population (from Dijkstra et al. 1990), the trend predicted by the population genetic simulation model of Daan et al. (1996), and the ESS trend from the present model. Clearly, the trends predicted by both models agree very well with each other, and they fit the field data quite closely.

ESS Intercept and Slope

To complete our analysis of linear sex ratio trends, we allow both the slope β_1 and the intercept β_0 to vary. To find an evolutionarily stable combination (β_0^*, β_1^*), the ESS condition (eq. [20]) must be solved twice: once for the intercept β_0^*, given a slope β_1^*, and once for the slope β_1^*, given an intercept β_0^*. It can be shown that both conditions cannot be fulfilled at the same time. We do not give an analytical proof, but the result is illustrated in figure 2,
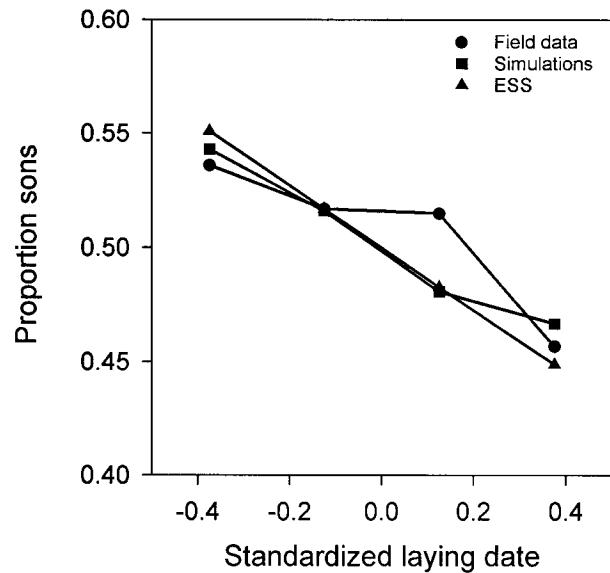

Figure 3: Comparison of three seasonal sex ratio trends in the kestrel: the trend observed in the field (Dijkstra et al. 1990), the trend predicted by the genetic simulation model of Daan et al. (1996), and the trend predicted by the ESS model, assuming a linear sex ratio trend with fixed midseason sex ratio $\beta_0 = 1/2$.

which shows that the curves defined by the ESS slope β_1^* given an intercept β_0^* and the ESS intercept β_0^* given a slope β_1^* do not intersect in the (β_0^*, β_1^*) plane.

Result 4. For the model where the sex ratio $\sigma(t)$ depends linearly on laying date t according to $\sigma(t) = \beta_0 + \beta_1 t$, there exists no evolutionarily stable combination (β_0^*, β_1^*).

Even if there exists no ESS, one can infer from the selection differentials the general direction of evolution, as illustrated in figure 2. This suggests that β_0^* and β_1^* are expected to evolve to ever lower values, eventually leading to a bang-bang strategy. To test this expectation, we ran some Monte Carlo simulations corresponding to our model, where β_0 and β_1 were coded for by two unlinked loci with additive interaction of the alleles per locus. At the start of the simulations, all 800 breeding individuals were homozygous for the alleles corresponding to $\beta_0 = 0.5$ and $\beta_1 = 0$. The simulation model corresponds to that of Daan et al. (1996) but also includes mutation. With probability 0.001 per allele and per generation, alleles mutated to slightly different values (mutation steps drawn at random from the interval $[-0.1, 0.1]$). Simulations were run for 500,000 generations. The results are summarized in figure 4. Two main conclusions emerge. First, the expectation based on the geometrical argument in figure 3 is born out, but evolution proceeds very slowly given the large number of generations and the fairly high mutation rate. Second, the predictive power of the model is rather
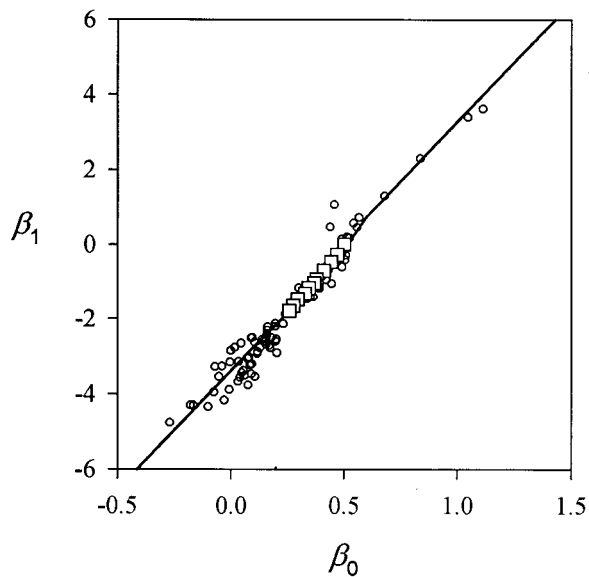
Figure 4: Results of 100 simulation runs of the genetic model implementing linear sex ratio trends. The two curves from figure 2 are almost undistinguishable on this scale. Squares represent the population averages of β_0 and β_1 after every 50,000 generations. These averages move slowly but monotonically along the lines predicted by the ESS model. Circles represent the individual simulation outcomes after 500,000 generations.

limited. Individual simulation runs vary enormously, and even after 500,000 generations, there are still simulations with a positive rather than a negative slope. Apparently, selection is so weak that forces such as drift and mutation dominate the outcome. This was confirmed by running the simulations with biased mutations, which had a large impact on the simulation outcomes (not shown here).

The absence of an ESS in the model could have been circumvented by choosing a different parametrization, as pointed out by an anonymous referee. For example, a piecewise linear sex ratio trend can also be characterized by the two numbers t_0 and t_1, where $\sigma(t_0) = 0$ and $\sigma(t_1) = 1$. Now bang-bang strategies are feasible within the model (given by $t_0 = t_1$), and it is easy to derive that the strategy characterized by $t_0^* = t_1^* = -0.154$ is the unique ESS (see Result 1). Hence, the parameterization of the strategies has important consequences for the model outcome. The (β_0, β_1) parameterization does not admit an ESS since bang-bang strategies are not feasible because they correspond to infinitely large parameter values. However, the (t_0, t_1) parameterization has a drawback in that a constant sex ratio, independent of laying date, corresponds to infinitely large parameter values. Hence, the most parsimonious ancestral state of a constant sex ratio cannot be represented by this parameterization. Anyhow, Monte

Carlo simulations again indicate an enormous variation between simulation runs. If the ESS is reached at all, this happens only after a very long time.

ESS with Mechanistic Constraints

Up to now, the choice of strategy set was rather ad hoc and not motivated by mechanistic considerations. Even though we do not know the mechanisms underlying sex ratio control in birds, we can make some educated guesses. Suppose females can identify the sex of an egg after some point during egg development. It is then conceivable that female birds might be able to adjust the sex ratio before laying by discarding developing eggs of the undesired sex. This is unlikely to be entirely cost free. Even if a female can resorb eggs and is able to recycle the material without losses, it takes time to develop an extra egg to replace the discarded egg. Adjusting the sex ratio by these means may thus result in a delay in average laying date. Because clutch size and juvenile survival decline systematically with laying date in the kestrel (see table 1), as indeed in most other single-brooded bird species of the temperate zone (Klomp 1970), a delay caused by sex ratio control has direct negative consequences for offspring fitness.

We shall consider two scenarios of this type of control. In the first, females may discard any egg of the undesired sex and every discarded egg results in a delay in laying date by a fraction d of the breeding season. In the second scenario, the female can discard only the first eggs, also resulting in a delay by a fraction d, but once she has started laying, no eggs between the first laid and the last laid can be discarded. This scenario was motivated by the observation that in several species of raptors only the first-laid egg exhibits a seasonal sex ratio trend (I. Pen, unpublished data; C. Dijkstra, personal communication).

Finding the ESS sex ratio trend with this type of constraint is computationally more cumbersome, and we refer to appendix B for the technical details of the dynamic optimization procedure we employed.

Again, life-history parameters of the model are estimated from field data of the Dutch kestrel population (table 1). The only unspecified parameter in the model is the average delay d in laying date that results from biasing the sex ratio by discarding and replacing one egg of the undesired sex. In kestrels, eggs are normally laid every other day. Therefore, it is reasonable to assume that the maximum value of d is obtained if it would take two whole days to replace a discarded egg by a new one. Since the range of laying dates of kestrels in our study area is about 50 d, the maximum value of d as a fraction of the breeding season is about 0.04.

Without any costs ($d = 0$), the optimal sex ratio trend for the first scenario is, as expected, a bang-bang strategy:
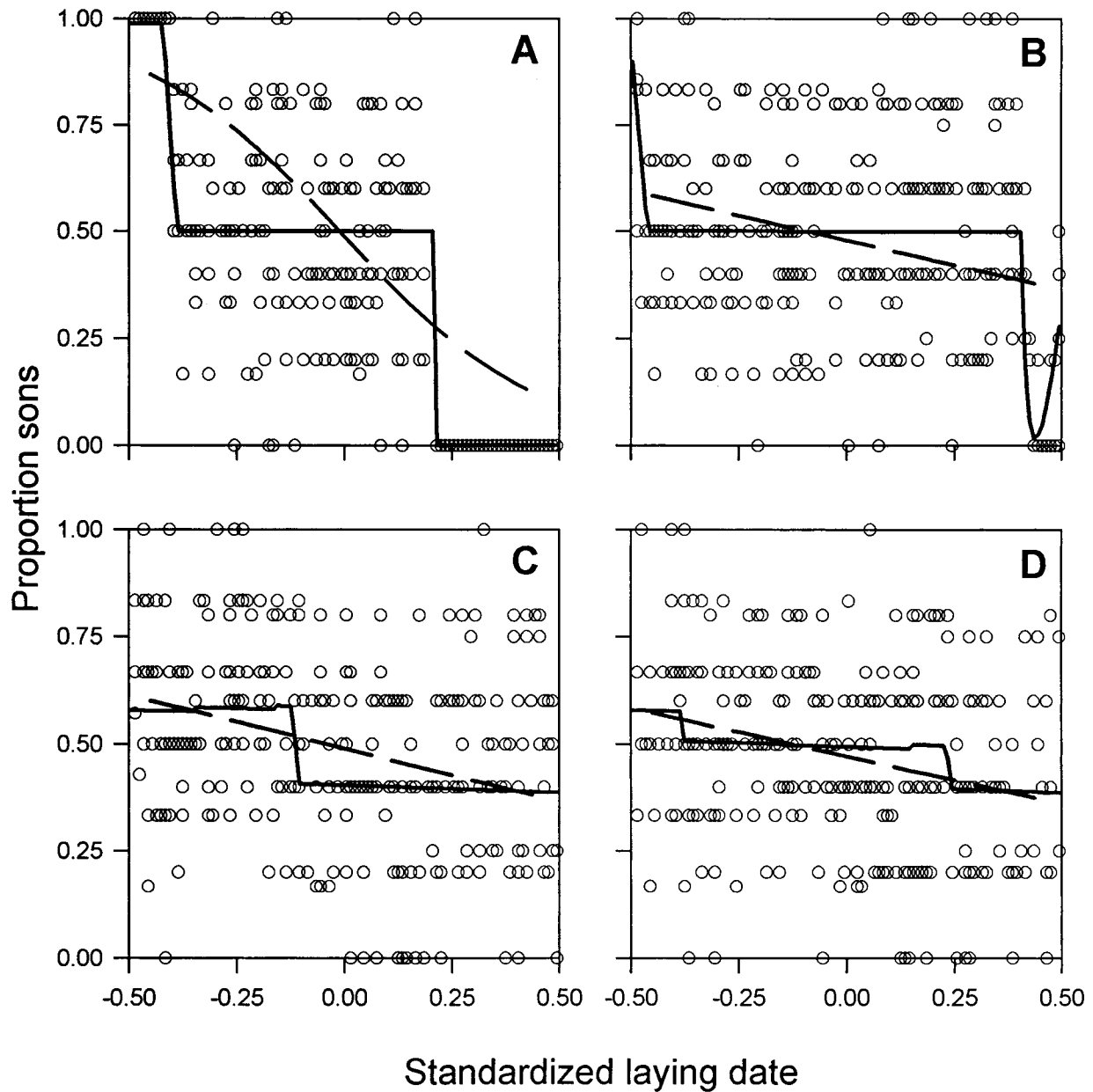
Figure 5: Examples of ESS sex ratio trends for the mechanistic model. Lines indicate the ESS trends; open circles represent brood sex ratios sampled at random ($N = 300$) from the ESS trends; dashed lines indicate logistic regression models fitted to the simulated samples. *A*, *B*, Examples of the scenario where a female can control the sex ratio of any egg. *C*, *D*, Examples of the scenario where a female can only affect the sex ratio of the first egg. Values of the delay d (as fraction of the breeding season) in laying date caused by resorbing and replacing an egg containing the undesired sex: *A*, *D*, $d = 0.01$; *B*, $d = 0.013$; *C*, $d = 0$.

a switch from producing only sons to producing only daughters at $\tau^* = -0.154$ (see Result 1). For the scenario in which only the first-laid egg can be biased, the result is qualitatively the same, except that the magnitude of the deviation from an even sex ratio is considerably smaller. For values of $d > 0$, the optimal sex ratio trends have a "bang-bang-bang" shape; first produce more or only sons, then switch to an even sex ratio, then switch to producing more or only daughters. However, for values of $d > 0.016$, considerably smaller than the maximum $d = 0.04$, it never pays to bias the sex ratio at any time in the season.

Result 5. Given the maturation time hypothesis, only

if the delay in laying date caused by discarding and replacing one egg of the undesired sex is smaller than $d \approx 0.016$ (≈ 0.8 d) is it adaptive to bias the sex ratio in some part of the season. The sex ratio trend observed in the kestrel is fitted best for a delay of $d = 0.0128$.

Figure 5 shows some examples of optimal sex ratio trends for different values of d and for both scenarios of control. Also shown are typical examples of simulated samples taken from populations with optimal sex ratio trends. The results are fitted by logistic regression models. This serves to demonstrate that even if a bang-bang-bang-like strategy is in fact real, it will often prove very hard to distinguish the corresponding empirical data from a more gradual or even linear trend. In order for an optimal sex ratio trend to emerge that is statistically significant ($p < .05$ in 90% of simulations, tested by log-likelihood ratio test after logistic regression) when 300 broods are sampled uniformly across the season (roughly the sample size of the observed trend in the kestrel; see Dijkstra et al. 1990), d must be smaller than 0.013 ($\approx 2/3$ d to produce a new egg).

Figure 6 shows how the ESS predictions of the mechanistic model depend on the five life-history parameters used for the predictions. We assumed the value of $d = 0.0128$ that fits the kestrel's sex ratio trend most closely. Each parameter was varied between 75% and 125% of its estimated value (table 1), keeping the other parameters constant at their estimated value. For an array of parameter values in this range, the ESS sex ratio trend was calculated and a logistic regression curve was fitted to a corresponding simulated sample of 2,000 broods. Note that for sex ratios not too far from 1/2, a logistic regression curve $\{1 + \exp[-(\delta_0 + \delta_1 t)]\}^{-1}$ is indistinguishable from a linear regression line $\beta_0 + \beta_1 t$. Since $(1 + \exp[-y])^{-1} = 1/2 + 1/4y + O(y^2)$, the slope parameter of a logistic regression is about four times the slope of a linear regression; that is, $\delta_1 \approx 4\beta_1$. Figure 6 shows how the slope parameter of the logistic regression changes with the parameter values. Apparently, the predictions are most sensitive to changes in seasonal variation in recruitment. As the relative rate of decline in recruitment with laying date (measured by r_1/r_0) becomes more pronounced, the slope of the sex ratio trend quickly becomes shallower. This is not surprising, given that in the model the cost of sex ratio control is directly proportional to the seasonal decline in recruitment.

Discussion

The Fitness Concept

In stage structured populations, the fitness concept has to be based on population dynamical considerations (e.g.,
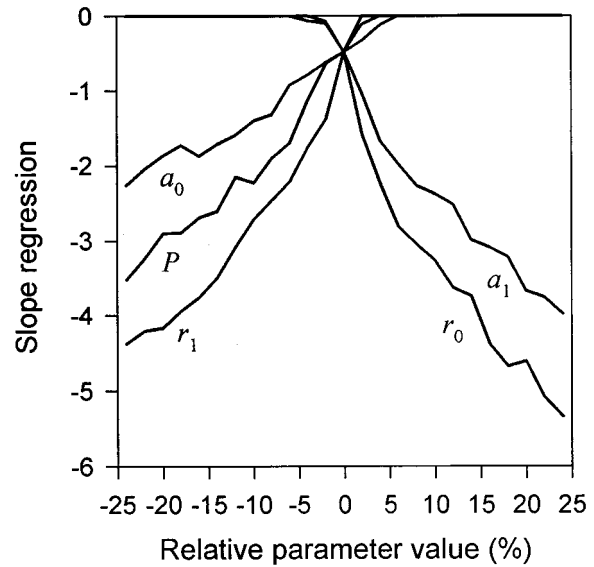

Figure 6: Sensitivity analysis of the mechanistic model. Each of the five life-history parameters in the model was varied between 75% and 125% of their estimated values (see table 1); the other parameters were kept constant at their estimated value. For the resulting parameter combinations, simulated samples were taken from the ESS sex ratio trend and fitted by a logistic regression curve. The figure shows the slope parameter δ_1 of the logistic regression, indicating the steepness of the ESS sex ratio trend. The delay parameter was kept constant at $d = 0.0128$.

Charlesworth 1994). An ESS analysis then boils down to comparing the growth rate of a subpopulation of mutants with the growth rate of the resident population at large (e.g., Taylor 1996). Often the analysis focuses on a trait that is expressed in only one stage of the life history, and then one may equivalently use reproductive value as a measure of fitness. In the analysis presented here, we demonstrate how in such a situation the additional complexities arising from a seasonal environment can be dealt with relatively easily. One simply derives how the seasonal average of a trait depends on the seasonal distribution of the trait. The analysis then proceeds as if there were no seasonality. This approach is justified whenever there is no between-season correlation in the timing of breeding.

In our analysis, we have assumed that the population growth rate is density independent; that is, we allowed the ESS population to have a growth rate different from unity. For the kestrel, our models yield an ESS growth rate of $\lambda^* \approx 1.2$, which suggests that the underlying field data were obtained from a source population. On an evolutionary time scale, no closed population can have a growth rate that consistently exceeds unity. In principle, we could have incorporated density dependence in our models, leading to the additional constraint $\lambda^* = 1$. However, the specific

proximate way in which life-history parameters are affected by density dependence can have important implications for evolutionary predictions (Mylius and Diekmann 1995). The sensitivity analysis summarized in figure 6 shows that different parameters can have quite different effects on the ESS outcome. It is therefore hard to tell how density dependence would have affected our results. We have not included density dependence in our model, since in the kestrel little is known about the details of population regulation. Besides, little is known about what constitutes a good fitness measure in the context of density-regulated source-sink populations.

The Strategy Set

As our results confirm, the choice of strategy set in evolutionary optimization models may have strong effects on the model predictions. Unfortunately, progress is hampered by the fact that usually very little, if anything, is known about the mechanistic constraints acting in real-world systems. There are two common approaches to dealing with this unfortunate situation. The easiest way out is simply to assume that no constraints are limiting phenotypic expression. The other approach is to adopt some ad hoc constraints, often also guided by considerations of simplicity rather than biological realism. In our application to the seasonal sex ratio trend of the kestrel, we have approached the problem by considering a suite of different strategy sets, ranging from a model with no constraints at all, via simple low-dimensional strategy sets, to more complex strategy sets with explicit incorporation of some plausible mechanisms of sex ratio control. We believe this approach has several advantages. First of all, it makes it possible to judge the robustness of model predictions to changes in the strategy set. For example, for linear sex ratio trends, we found an ESS when only one parameter was varied, whereas no ESS exists when the second parameter was allowed to vary simultaneously. Hence, this model is apparently not structurally stable in the sense that addition of one more degree of freedom to the strategy set alters the outcome completely. Moreover, the outcome is strongly dependent on the parameterization. Furthermore, the mechanistic strategy set indicated that addition of a small cost of sex ratio control may alter the structure of the optimal strategies significantly.

Another advantage of this approach is that it may generate new, testable predictions. This kind of "inverse optimality" method (McFarland 1977) is illustrated by the mechanistic model, in which we have explicitly included a plausible mechanism of sex ratio control and associated costs in terms of a delay in laying date. We found that in order for the maturation time hypothesis to be a sufficient explanation for the observed sex ratio trend in the kestrel,

the maximum delay in laying date caused by sex ratio control must be surprisingly small (<2/3 d).

Our simulated samples taken from populations with optimal sex ratio trends predicted by the mechanistic model illustrate another important point: even if a bang-bang-bang-like optimal strategy with multiple switch points is in fact real, it may be very hard to verify this empirically. Figure 5 clearly shows that such strategies can easily be mistaken for more gradual or even linear trends.

Phenotypic versus Genetic Models

Broadly speaking, there are two rather different approaches to study adaptive evolution: the dynamic approach of population genetics (e.g., Karlin and Lessard 1986) and the static ESS approach of evolutionary game theory (Charnov 1982; Maynard Smith 1982). Unfortunately, the two approaches can lead to different and even contradictory conclusions. The question of which approach is more adequate and whether they can be reconciled is currently a hot topic in theoretical population biology (Eshel 1996; Hammerstein 1996; Weissing 1996). It is interesting that for linear sex ratio trends with fixed intercept the ESS model presented here and the population genetic model of Daan et al. (1996) yield very similar predictions. For the case of linear sex ratio trends with intercept and slope both variable, we also find such agreement. However, the outcomes of individual simulation runs of the genetic model are variable to such an extent that its predictive power is close to negligible. This is in line with the conclusion we reached from the mechanistic model: that a very small cost is sufficient to overcome the selective advantage of biasing the sex ratio. In the genetic model, selection is apparently so weak that nondeterministic processes such as drift and mutation may dominate the outcome.

We think it may in general be a worthwhile endeavor to apply both the ESS and the genetic approach to the same empirical problem. An advantage of the ESS approach is that it is easier to investigate the robustness of predictions with respect to changes in both the number and the values of model parameters. However, genetic simulation models give much more insight into the predictive power of a particular hypothesis because they generate a distribution of predictions.

Concluding Remarks

As with all studies applying an optimization approach to a real-world system, we are facing a number of general problems. Some authors (e.g., Gould and Lewontin 1979) have claimed that with the benefit of hindsight it is always possible to construct an optimality model that fits a given set of observations well. Although we agree to a certain

extent, this does not render optimality models useless. In our case, for example, the models can be used to derive clear-cut a priori predictions for other kestrel populations. As indicated by the sensitivity analysis depicted in figure 6, the steepness of seasonal sex ratio trends should be inversely related to the steepness of the seasonal decline in recruitment. It seems likely that the seasonal decline in recruitment is steeper for populations at higher latitudes, and therefore we would expect the steepness of seasonal sex ratio trends to decrease with latitude. We are currently collecting sex ratio and life-history data in kestrel populations at several latitudes to evaluate this expectation. In line with our expectation, it has been discovered in the meantime (Smallwood and Smallwood 1998) that a population of American kestrels (*Falco sparverius*) in Florida exhibits a seasonal sex ratio trend, whereas a more northern population in Canada lacks a seasonal trend in the brood sex ratio.

Another obstacle is our general ignorance with respect to the factors constraining control in natural systems. In our opinion, the most promising avenue of progress is the explicit implementation of hypothetical mechanisms of control. Besides making the costs of control explicit, this approach has the advantage that it generates new, testable predictions via the inverse optimality method. In our case, the mechanistic model has identified how large a cost would suffice to refute the maturation time hypothesis as the explanation for the observed sex ratio trend in the kestrel.

Acknowledgments

APPENDIX A

Maximization of Reproductive Value

In this appendix, we verify that maximizing reproductive value and maximizing population growth rate identify the same evolutionary equilibria when a phenotypic trait is expressed in only one stage of the life history.

Recall that a necessary condition for evolutionary stability of a monomorphic resident population with phenotype s^* against invasion attempts by mutants with phenotype s is provided by comparing the growth rate of the mutant subpopulation with the growth rate of the resident population:

$$\lambda(s, s^*) \leq \lambda(s^*, s^*). \tag{A1}$$

This amounts to maximizing $\lambda(s, s^*)$ with respect to s. Thus, we need to inspect the derivative of $\lambda(s, s^*)$ with respect to s. It can be shown (see Taylor 1996) that the sign of $\partial\lambda/\partial s$ is the same as the sign of

$$\boldsymbol{v}^* \frac{\partial \mathbf{B}}{\partial s} \boldsymbol{u}^* = \sum_{i,j} v_i^* \frac{\partial}{\partial s} b_{ij}(s, s^*) u_j^*, \tag{A2}$$

where $\boldsymbol{v}^*$ is the row vector of reproductive values of the different stages in the resident population, which is given by a dominant left eigenvector of $\mathbf{B}(s^*, s^*)$, and $\boldsymbol{u}^*$ represents the stable stage distribution of the resident population, given by a dominant right eigenvector of $\mathbf{B}(s^*, s^*)$. If the mutant behavior s is restricted to stage 1, then b_{ij} does not depend on s for $j \neq 1$, and equation (A2) reduces to

$$u_1^* \sum_i v_i^* \frac{\partial}{\partial s} b_{i1}(s, s^*). \tag{A3}$$

The zeros of this quantity are identical to the extrema with respect to s in $s = s^*$ of

$$v_1(s, s^*) = \frac{1}{\lambda^*} \sum_i v_i^* b_{i1}(s, s^*). \tag{A4}$$

This may be viewed as the reproductive value of an individual displaying mutant behavior in stage 1 during one time step.

APPENDIX B

Dynamic Optimization Procedure

This appendix contains a description of the procedure employed to compute the evolutionarily stable sex ratio trends in the model with mechanistic constraints.

Suppose a female decides at time t in the season to produce a sex ratio $\sigma(t)$. This will result in a delay in laying date by an amount Δt, and the adjusted laying date is given by $t' = t + \Delta t$. The ESS sex ratio trend is then, for every time t a female maximizes her reproductive value,

$$v_f(t) = c(t)\{[1 - \sigma(t)]v_d(t') + \sigma(t)v_s(t')\}, \tag{B1}$$

where $v_d(t')$ is the reproductive value of a daughter born at time t', and $v_s(t')$ the reproductive value of a son born at time t'.

How do we find the adjusted laying date t'? Let $\Delta\sigma(t) = |\sigma(t) - 1/2|$ denote the sex ratio bias away from parity. The probability that an egg contains the "undesired" sex is 1/2, and resorbing it delays the laying date by a fraction d of the breeding season. The larger the clutch size $c(t)$, the more eggs need to be discarded in order to achieve a given bias $\Delta\sigma(t)$. Hence, the average delay Δt is given by

$$\Delta t = \frac{1}{2} dc(t)\Delta\sigma(t). \tag{B2}$$

How do the offspring reproductive values depend on laying date? Since the age of first breeding of a daughter is not influenced by laying date, the relative reproductive value $v_d(t)$ of a daughter born at time t in the season only depends on the first-year survival probability as a function of birth date t:

$$v_d(t) = s_0(t). \tag{B3}$$

The reproductive value of a son born at time t depends on the probability he will start breeding in the next year, and it is given by

$$v_s(t) = s_0(t)\{[1 - \alpha(t)]v_2^* + \alpha(t)v_3^*\}. \tag{B4}$$

Here $v_2^* = R^*P/\lambda^*$ and $v_3^* = R^*$ are the reproductive values of nonbreeding and breeding males, respectively.

We use the following procedure to find the sex ratio trend $\sigma^*(t)$ that maximizes $v_f(t)$ for every t (e.g., McNamara et al. 1997). Start with an arbitrary initial sex ratio trend, say $\sigma_0(t) = 0.5$ for every t. Compute for this trend the seasonal averages $\bar{\sigma}$ and $\bar{\alpha}$, given by equations (9) and (11), respectively. These values are then used to calculate R^* and λ^*, which appear in expression (B4). Then proceed to find for every t the sex ratio $\sigma_0'(t)$ that maximizes $v_f(t)$, the best reply to $\sigma_0(t)$. Repeat this procedure with an updated sex ratio trend $\sigma_1(t)$ that is a weighed average of the previous sex ratio trend $\sigma_0(t)$ and the best reply $\sigma_0'(t)$: $\sigma_1(t) = (1 - \theta)\sigma_0(t) + \theta\sigma_0'(t)$. And so on, until convergence is obtained to a trend that is a best reply to itself and, therefore, a candidate ESS (strictly speaking, a Nash equilibrium). To prevent cycling of the iteration process, it may be necessary to choose a very small value of the weighing factor θ. Our results were obtained using a value of $\theta = 0.02$.

Literature Cited

Caswell, H. 1989. Matrix population models. Sinauer, Sunderland, Mass.

Cavé, A. J. 1968. The breeding of the kestrel *Falco tinnunculus* L. in the reclaimed area Oostelijk Flevoland. Netherlands Journal of Zoology 18:313–407.

Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, N.J.

Clutton-Brock, T. H. 1986. Sex ratio variation in birds. Ibis 128:317–329.

Daan, S., C. Dijkstra, and F. J. Weissing. 1996. An evolutionary explanation for seasonal trends in avian sex ratios. Behavioral Ecology 7:426–430.

Dijkstra, C. 1988. Reproductive tactics of the kestrel *Falco tinnunculus*: a study in evolutionary biology. Ph.D. thesis, University of Groningen, The Netherlands.

Dijkstra, C., S. Daan, and J. B. Buker. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. Functional Ecology 4:143–147.

Ellegren, H., L. Gustafsson, and B. C. Sheldon. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. Proceedings of the National Academy of Sciences of the USA 93:11723–11728.

Eshel, I. 1996. On the changing concept of population stability as a reflection of a changing point of view in the quantitative theory of evolution. Journal of Mathematical Biology 34:485–510.

Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. Proceedings of the Royal Society of London B, Biological Sciences 205:581–598.

Gowaty, P. A. 1990. Facultative manipulation of sex ratios in birds: rare or rarely observed? Current Ornithology 8:141–171.

———. 1993. Differential dispersal, local resource competition, and sex ratio variation in birds. American Naturalist 141:263–280.

Hammerstein, P. 1996. Darwinian adaptation, population genetics and the streetcar theory of evolution. Journal of Mathematical Biology 34:511–532.

Karlin, S., and S. Lessard. 1986. Theoretical studies on sex ratio evolution. Princeton University Press, Princeton, N.J.

Klomp, H. 1970. The determination of clutch size in birds. Ardea 58:1–124.

Komdeur, J., S. Daan, J. Tinbergen, and C. Mateman. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature (London) 385:522–525.

Lessells, C. M., A. C. Mateman, and J. Visser. 1996. Great

tit hatchling sex ratios. Journal of Avian Biology 27: 135–142.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

McFarland, D. J. 1977. Decision making in animals. Nature (London) 269:15–21.

McNamara, J. M., J. N. Webb, E. J. Collins, T. Szòkely, and A. I. Houston. 1997. A general technique for computing evolutionarily stable strategies based on errors in decision-making. Journal of Theoretical Biology 189: 211–225.

Mylius, S. D., and O. Diekmann. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos 74:218–224.

Olsen, P. D., and A. Cockburn. 1991. Female-biased sex allocation in peregrine falcons and other raptors. Behavioral Ecology and Sociobiology 28:417–423.

Parker, G. A., and J. Maynard Smith. 1990. Optimality models in evolutionary biology. Nature (London) 348: 27–33.

Smallwood, P. D., and J. A. Smallwood. 1998. Seasonal shifts in sex ratios of fledgling American kestrels (*Falco sparverius paulus*): the early bird hypothesis. Evolutionary Ecology 12:839–853.

Taylor, P. D. 1996. Inclusive fitness arguments in genetic models of behaviour. Journal of Mathematical Biology 34:654–674.

Weissing, F. J. 1996. Genetic versus phenotypic models of selection: can genetics be neglected in a long-term perspective? Journal of Mathematical Biology 34:533–555.