ORNIS SVECICA 13: 107–114, 2003 https://doi.org/10.34080/os.v13.22802

Population dynamics of the Swedish Ornithological Society

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Abstract

It has recently been recognized that there is declining interest in ornithology among the younger generations. In this paper we analyse the short and long-term dynamics of the Swedish Ornithological Society (SOF) and the Swedish Society for Nature Conservation (SNF) by using analytical tools from population ecology. We first show that the increasing number of SOF and SNF members is not the result of a constant proportion of ornithologists or people interested in nature conservation among a growing Swedish population. Hence, the number of members most likely reflects the true interest in joining organizations such as SOF. We also demonstrate that the growth rate of SOF can be fairly well estimated, but the possible equilibrium size is uncertain. Removing the long-term trend reveals a cyclic pattern with a period of 23 years. This pattern was not found when analysing the SNF data and we discuss the observed patterns in relation to human and member generation time. Finally, we present an improved population model based on data up to 1998 and show how model predictions compare with the observed number of members in year 2002.

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Received 26 June 2002, Accepted 2 December 2003, Editor: A. Hedenström

Introduction

Scandinavia has a long and successful history of ornithology. From the first documentation of different species and various aspects of bird life (e.g. Nilsson 1858), to the development of a modern theory of bird migration (Alerstam & Hedenström 1998), many researchers got their inspiration as well as knowledge about natural history from the study of birds. The Swedish Ornithological Society (SOF) – founded in 1945 – as well as Ottenby and Falsterbo Bird Observatories (founded in 1946 and 1955, respectively) have contributed significantly to the advancement of ornithology in Sweden.

Every now and then, concern is raised about the fluctuations in the number of SOF members (e.g. Källander & Svensson 1985, Svensson 1988). However, no serious attempts have been made to understand how the number of society members relates to the total Swedish population, i.e. the ”environment” for recruitment. Furthermore, little is known about the underlying dynamics of SOF, and hence nobody can separate short and long term fluctuations appearing as trends in data. Such knowledge is not only of interest for the ornithological society, but also for academic ecology relying on both long-term data sets collected by amateurs as well as recruiting students with a firm background in field ornithology. As such, this is a problem of general concern also to academic ecology.

Here we provide an analysis of the short and long-term dynamics of the Swedish Ornithological Society by using analytical tools borrowed from population ecology. We also provide a comparison with the

Swedish Society for Nature Conservation (SNF), established in 1909, which is the largest environmental organization in Sweden.

Material and methods

Data

We used a time series of the total number of SOF members 1945–1998, compiled from the annual reports of SOF published in the society's journal "Vår Fågelvärld". Unlike most ecological data, there is no reason here to assume any observation error. Hence, all variation in the time series can be attributed to the stochastic processes of recruitment of new and quitting of previous members. This simplifies the analysis considerably since all deviations between a model and data must be due to process error (Hilborn & Mangel 1997). The total human population in Sweden could potentially affect the number of members in SOF. To see whether the number and dynamics of SOF members simply reflects a constant proportion among a changing total population, we also used a time series of the Swedish population 1945–1998. Data on the Swedish population growth can be found at the Statistics Sweden's home page (http://www.scb.se). Finally, we used a time series of the number of members in the Swedish Society for Nature Conservation (SNF) – established in 1909 – for comparison to the dynamics of SOF.

Alternative Models

No population grows without bound, i.e. the per capita growth rate must decline as population size (number of members) goes up. The simplest model assumes a linear relationship between per capita growth rate and population size and is known as the logistic growth model. There are several ways of expressing a logistic-type model in discrete-time. One alternative often used in population studies of large mammals is the so-called Gompertz approach

$$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t)) \qquad (1)$$

where N_t is the number of members in year t, a_0 is the intrinsic growth rate, and a_1 is the strength of negative feedback. Note that there is a linear relationship between the logarithmic rate of change and the logarithm of population size.

Equation 1 may look simple but it can often describe ecological time series of mammals, birds and other organisms with reasonable accuracy. It is therefore interesting to investigate to what extent this equation is also a good model for the temporal dynamics of a society such as SOF. However, one could think of an extension of the model above before approaching data. Ultimately, the equilibrium population size will be limited by the size of the Swedish population size. To test whether the number of SOF members is affected by the size of the Swedish population we contrasted the model above with an alternative model where we also included the Swedish population, S, such that

$$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t) + b_1 \ln(S_t)) \qquad (2)$$

Parameter estimation and model selection

A stochastic version of the discrete time logistic model above (without the Swedish population size as a covariate) can be expressed as

$$N_{t+1} = \left[N_t \exp(a_0 + a_1 \ln(N_t))\right] \cdot W_t \qquad (3)$$

$$W_t = \exp\left(\sigma\varepsilon_t - \frac{\sigma^2}{2}\right) \qquad (4)$$

where W_t is the process error with standard deviation σ, and ϵ_t is a normal random deviate with zero mean and unit variance. The process error is assumed to be lognormal, a reasonable assumption when analysing populations (Hilborn & Mangel 1997). The maximum likelihood estimates of a_0 and a_1 are the values minimizing the negative log-likelihood with respect to a_0 and a_1:

$$L(a_0, a_1 \mid data) = \sum_{t=2}^{k} \ln(\sigma) + \frac{1}{2}\ln(2\pi) + \frac{d_t^{\,2}}{2\sigma^2} \qquad (5)$$

where d_t is the deviation between the observed and predicted ln-transformed number of members at time t.

A model with many parameters is more likely to explain the observed variation in data, but each parameter estimate will be more uncertain compared to simpler models. We therefore selected the best model based on the Akaike Information Criterion (corrected for small sample size) AIC_c (Burnham & Anderson 1998). The model having the lowest AIC_c is the most parsimonious model and is therefore to be preferred.

Results

Fitting the alternative models to the SOF data and ranking them according to how well they explained data with a minimum number of parameters (Table 1), show that including data on the Swedish population size does not help us to understand the fluctuations in SOF members. Put differently, the increase in the

Table 1. Alternative models, log-likelihood (Log L), number of estimated parameters (K), Akaike Information Criteria corrected for small sample size (AIC_c), and AIC_c differences ($\triangle_i = AIC_{ci}$ - min AIC_c) for the alternative models. N_t =Number of SOF members in year t, S_t = Number of Swedish citizens in year t.
Alternativa modeller, log-likelihood (Log L), antal skattade parametrar (K), Akaike Information Criteria korrigerade för låg provstorlek (AIC_c), samt AIC_c differenser ($\triangle_i = AIC_{ci}$ - min AIC_c) för de alternativa modellerna. N_t =Antal SOF-medlemmar år t, S_t = Sveriges befolkningsmängd år t.

Model	Log L	K	AIC_c	Δ_i
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t))$	86.8	3	-314.7	16.5
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t) + b_1 \ln(S_t))$	86.8	4	-312.4	18.9
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t) + a_2 \ln(N_{t-1}))$	96.3	4	-313.3	0.0

Table 2. Point estimates of all parameters in the alternative models.
Punktskattning av samtliga parametrar i de alternativa modellerna.

Model	a_0	a_1	a_2	b_1	σ
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t))$	0.32	0.97			0456
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t) + b_1 \ln(S_t))$	0.44	-0.032		-0.0083	0.046
$N_{t+1} = N_t \exp(a_0 + a_1 \ln(N_t) + a_2 \ln(N_{t-1}))$	0.15	0.51	-0.523		0.0380

number of SOF and SNF members are not a result of a constant proportion of ornithologists or people interested in nature conservation among the growing number of Swedish citizens (Figur 1A–B). Hence, the positive trend in the number of members since the foundation of SOF and SNF actually describes a true increase in the interest in joining organizations such as SOF and SNF.

Despite its simplicity, the logistic growth model provides a reasonable approximation of the long-term dynamics of SOF (Figure 1C). However, even though the model fit to data is good and the estimate of the intrinsic growth rate ($a_0 = 0.32$; Table 2) has a rather narrow confidence interval, we cannot estimate the feedback parameter ($a_1 = 0.97$) with any reasonable degree of certainty. That makes the estimate of the equilibrium size of SOF uncertain as well. An inspection of the deviations between model and data (not shown) reveals that there is information left in the residuals that has not been captured by the simple model. Before thinking about how to extend the model to account for all structured information in data, let us approach the time series a bit differently.

Both the SOF and the SNF time series have an increasing trend. While trends in time series may be interesting, removing them may give an idea about the underlying processes governing the fluctuations. We therefore fitted a first order polynomial to the SOF and SNF time series (after ln-transforming the data) and used the residuals for further analysis (Chatfield 1999). Removing a linear trend from the ln-transformed time series of SOF and SNF members, and plotting the residuals, highlights a seemingly periodic pattern, at least for the SOF data (Figure 2A). (We also tested to remove a non-linear trend by fitting a second order polynomial instead, but our general results did not change.) This observation is confirmed by inspection of the correlogram indicating a period of 23 years in the detrended SOF data (Figure 2B). The correlogram of SNF, on the other hand, has no clear periodic pattern but shows a very slow decay of autocorrelation indicating dominance of low frequent variation.

So, how could we improve the logistic model to

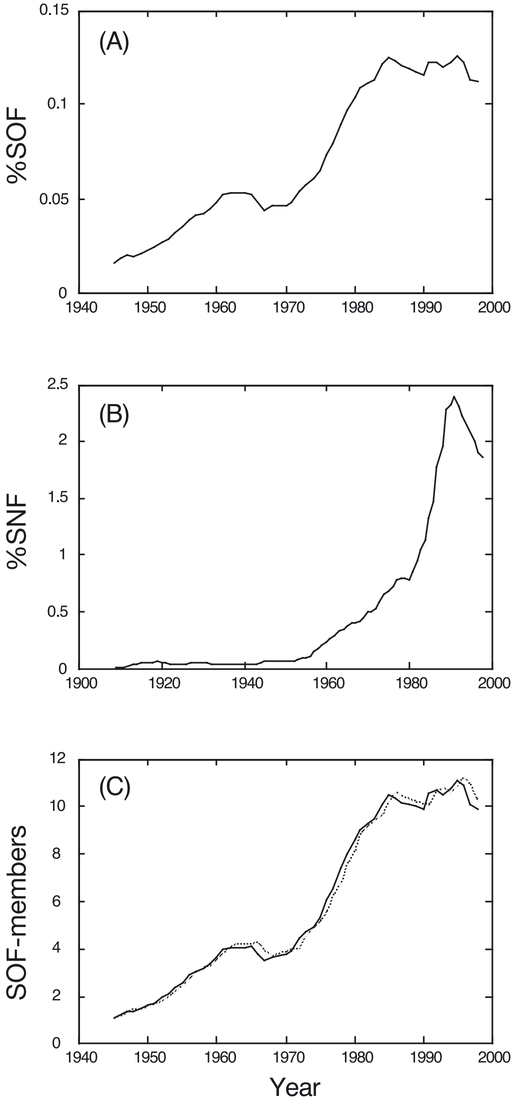


Figure 1. (A–B) The percentage of the Swedish citizens that are members of the Swedish Ornithological Society (SOF) or the Swedish Society for Nature Conservation (SNF). (C) The number of SOF members (solid line) and the best fit of the logistic growth model (dashed line). The point estimates of a and b are 0.32 and 0.97, respectively (see Table 2).

(A–B) Procentuell andel av Sveriges befolkning som är medlemmar av Sveriges Ornitologiska Förening (SOF) eller Svenska Naturskyddsföreningen (SNF). (C) Antal SOF- medlemmar (heldragen linje) och bästa anpassningen av den logistiska tillväxtmodellen (streckad linje). Punktskattningen av a respektive b är 0.32 och 0.97 (se Tabell 2).

better represent the temporal dynamics of SOF members? The periodicity demonstrated above tells us that we should include a delayed feedback term (e.g. Royama 1992) such that

$$N_{t+1} = \left[N_t \exp(a_0 + a_1 \ln(N_t) + a_2 \ln(N_{t-1}))\right] \cdot W_t \qquad (6)$$

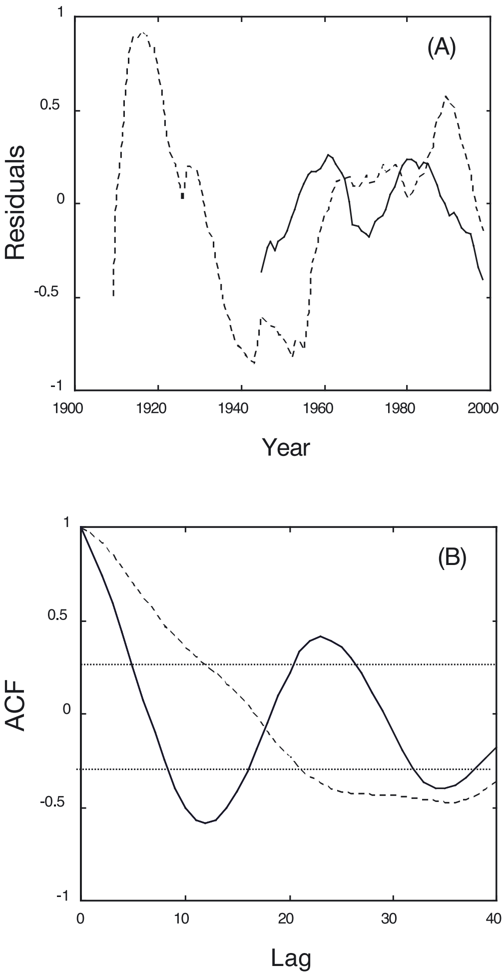
This model can give rise to a wide range of dynamics and when fitted to the SOF data it provides an improved fit (Figure 3A, Table 1). A new inspection of the residuals confirmed that there is no longer any significant structure left to be explained and we have finally found an acceptable model, at least from a statistical point of view.

During the course of this study, new data points on the number of SOF members became available and that offered an opportunity to see how well the model above could predict the future dynamics of SOF. In Figure 3B we present a histogram showing the predicted number of members in 2002, the last year from which we have data, together with the actual number of members in that year. The observed value is close to the median of the predictions and falls clearly within the 95% confidence interval.

Discussion

In order to understand complex patterns such as the number of SOF members, the underlying processes have to be revealed. Though it is trivial that the number of members has increased from the starting value in 1945, it could not be known *a priori* whether the temporal dynamics could be partly explained by the total number of Swedish citizens, i.e. the environment for recruiting new members. Interestingly, the upward trend since the establishment of SOF (and SNF) is independent of the total Swedish population. Since the post-war period, awareness about environmental issues has arisen. A number of environmental problems – including bioaccumulation of organic pesticides such as DDT and PCB, deforestation of tropical rainforest, and global climatic change – have gained large attention in media and public debates. This increasing concern about nature and the environment is probably mirrored in the increasing trend of SOF and SNF members.

Even though the logistic model describes the data reasonably well, the autocorrelated residuals indicate that the renewal function ought to be more complicated than assumed in the logistic growth model. Adding a second-order effect (another time lag) turned out to be a better representation of the dynamics, including the periodicity, and also



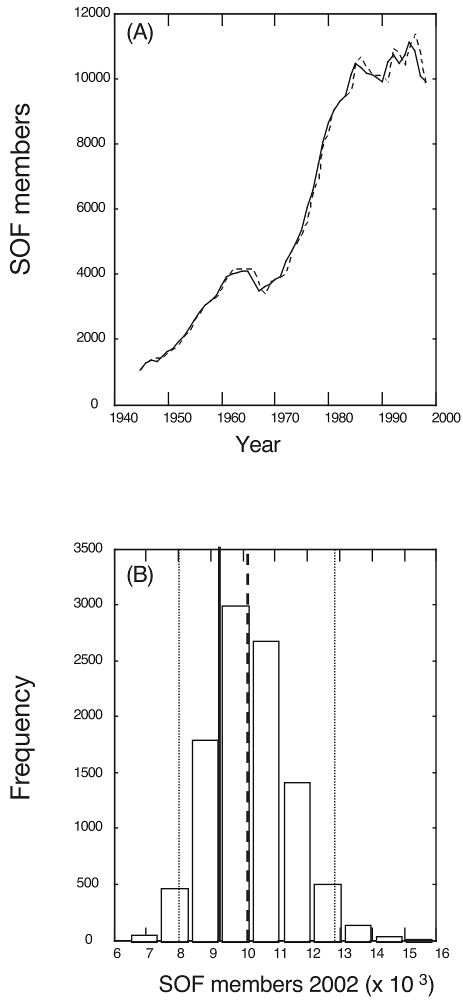


Figure 2. (A) Residual plot after removing a linear trend from the time series of members of the Swedish Ornithological Society (solid line) and the Swedish Society for Nature Conservation (dashed line). (B) Correlogram of the residuals in (A) showing a 23-year cycle in the Swedish Ornithological Society (solid line) and strongly autocorrelated fluctuations the Swedish Society for Nature Conservation (dashed line). Values outside the interval indicated by dotted lines are considered significantly different from zero.

(A) Residualer efter borttagandet av en linjär trend från tidsserien över medlemsutveckling i Sveriges Ornitologiska Förening och Svenska Naturskyddsföreningen (streckad linje). (B) Korrelogram baserat på residualerna i (A) som visar en 23-års cykel hos Sveriges Ornitologiska Förening (heldragen linje) och starkt autokorrelerade fluktuationer hos Svenska Naturskyddsföreningen (streckad linje). Värden utanför de streckade linjerna anses vara signifikant skilda från noll.

Figure 3. (A) The number of SOF members (solid line) and the best fit of the delayed logistic growth model (dashed line) $N_{t+1}=N_t exp(a_0+a_1N_t+a_2N_{t-1}$.(B) Histogram showing the predicted number of members in 2002, based on 10,000 iterations of the delayed logistic model. The observed value (thick solid line) is close to the median of the predictions (thick dashed line) and falls clearly within the 95% confidence interval (thin dotted lines).

(A) Antal SOF-medlemmar (heldragen linje) och bästa anpassningen av den logistiska tillväxtmodellen med fördröjd återkoppling mellan tillväxttakt och medlemsantal (streckad linje) $N_{t+1}=N_t exp(a_0+a_1N_t+a_2N_{t-1}$. *(B) Histogram som visar det predikterade antalet SOF medlemmar 2002 baserat på 10 000 iterationer av den logistiska tillväxtmodellen med fördröjd återkoppling mellan tillväxttakt och medlemsantal. Det observerade antalet medlemmar år 2002 (tjock heldragen linje) ligger nära medianvärdet av predicktionerna (tjock streckad linje) och faller inom det 95%-iga konfidensintervallet (tunna streckade linjer).*

managed to predict the number of members four years ahead with reasonable accuracy. The periodic fluctuations underlying the upward trend are probably due to two sources of demographic variation. Firstly, most populations (including SOF) consist of members of different age. It is generally appreciated that generation time is a key factor when analysing the dynamics of larger mammals (e.g. Caswell 2001). In the same way, there is of course a generation time in human populations (around 20–30 years). We note that this coincides with the observed periodicity in the number of SOF members after the long-term trend has been removed. This clear pattern is, however, not found in SNF and indicates that the explanation is more complicated. Maybe the relatively slow dynamics (dominance of low frequent variation) of SNF mirror the broader scope of SNF compared to SOF? It could be that a society specialized in ornithology is more sensitive to cohort effects (due to age-structure among the members and domination of certain age classes among the recruits) than a more generally oriented society such as SNF? In this paper we have described the temporal dynamics of SOF and identified some differences when compared to the temporal dynamics of SNF. Future work should possibly analyse age-structured data to be able to understand why the SOF and SNF dynamics are different.

Secondly, the development of societies based on voluntary contributions initially relies on single individuals. During the life of the society, these fiery spirits continue to play an important role in attracting new members and improve the structure and activities of the society. Such "key persons" are not likely to be as active and important after a number of years (sic!). In fact, they will most likely be replaced by a new generation of ornithologists. This turnover will further contribute to the variation in the potential for recruiting new members.

Occasionally, concern has been put forward regarding the member status of SOF (Svensson 1988) or the general problem of declining interest in ornithology among the younger generations (Svensson 1997). According to this study, SOF is again facing a generation shift. The last shift was in the 1960's and was entitled "the lost generation" (Källander & Svensson 1985). We think it is inevitable that societies such as SOF experience generation shifts. That is not, however, to argue that nothing can be done to recruit new members and make the society more attractive. On the other hand, identifying these shifts should alert SOF to more actively bridge the generation gap.

Acknowledgement

We are grateful to Märta Sundström at the Swedish Society for Nature Conservation (SNF) for providing the time series data on the number of SNF members. Anders Hedenström and an anonymous referee provided valuable comments that improved this paper. Niclas Jonzén was funded by the Center of Excellence in Evolutionary Ecology at the Department of Biological and Environmental Science, University of Jyväskylä.

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Sammanfattning

Populationsdynamiken i Sveriges Ornitologiska Förening

Sveriges Ornitologiska Förening (SOF) har en viktig plats att fylla inom svensk ornitologi. Dels som en kraft som aktivt verkar för ett ökat naturintresse och bevarande av värdefull biodiversitet, dels som en kraft som uppmuntrar och bedriver amatörforskning. För att göra detta behöver föreningen aktiva medlemmar som verkar för att genomföra föreningens mål. Inom SOF har det understundom framförts farhågor om medlemsutvecklingen i föreningen (Källander & Svensson 1985, Svensson 1988, Svensson 1997), men inget samlat grepp har tagits för att i detalj studera de faktorer som styr denna utveckling. Denna analys är ett försök att studera de processer som styr utvecklingen över en längre tidsperiod och att identifiera kritiska punkter där föreningen aktivt kan verka för att få en positiv utveckling.

Material och metoder

Den ekologiska forskningen har givit oss ett antal verktyg för att studera populationsutveckling hos vilda djurpopulationer. En förening med medlemmar kan grovt sett ses som en population där påbörjat medlemskap är en födsel och utträde samma sak som ett dödsfall. En praktisk sak som underlättar vid analysen är att vi inte behöver räkna med något mätfel, och att variationerna i tidsserien därmed består av stokastiskt inflöde och utflöde av medlemmar. Medlemsantalet varje år har fåtts från föreningens tryckta årsrapport, som jämförelse har även Svenska Naturskyddsföreningens (SNF) medlemsutveckling studerats. Data på Sveriges befolkningsmängd har tagits från Statistiska Centralbyråns hemsida (http://www.scb.se).

För att skatta tillväxthastighet och negativ återkoppling – vilka tillsammans påverkar den dynamiska jämviktsstorleken för SOF – använde vi oss av en logistisk tillväxtmodell och maximum likelihood metoden. Vi testade även om tillväxttakten påverkades av Sveriges populationsstorlek.

Resultat

Figur 1A och 1B visar att ökningen av medlemmar i SOF och SNF inte enbart beror på den ökande svenska befolkningen, utan avspeglar ett ökande intresse för medlemsskap i SOF. Detta bekräftas genom att visa att den logistiska tillväxtmodellen förklarar data lika bra med eller utan inverkan av Sveriges befolkningstäthet på tillväxthastigheten (Tabell 1). Den logistiska tillväxtmodellen fångar den observerade medlemsutvecklingen väl (Figur 1C) och skattningen av tillväxthastigheten (a_0 = 0.32) har ett relativt snävt konfidensintervall (ej visat). Styrkan av negativ återkoppling (a_1) skattades till 0.97 men att döma av konfidensintervallet är skattningen osäker, vilket därmed gör det svårt att uttala sig med säkerhet om jämviktsstorleken för SOF.

Även om den anpassade modellen beskriver medlemsutvecklingen på ett ganska tillfredställande sätt finns det systematiska avvikelser mellan modell och data. För att bättre förstå hur modellen skulle förbättras valde vi att närma oss data på ett kompletterande sätt. SOF's tidsserie domineras av en positiv trend men ofta kan det vara intressant att analysera även korttidsvariation. Vi valde därför att anpassa en linjär kurva (vi testade även ett andragradspolynom utan större skillnad) till ln-transformerade data och analysera residualerna med avseende på periodicitet. Efter att trend borttagits visar SOF data fluktuationer med en periodicitet på 23 år, medan motsvarande mönster saknas för SNF.

De mer eller mindre periodiska fluktuationerna runt den uppåtgående trenden i SOFs medlemsantal indikerar att den logistiska tillväxtmodellen bör byggas ut med en fördröjd återkoppling mellan tillväxttakt och medlemsantal. Den nya modellen har en mycket högre förklaringsgrad än den tidigare modellen (Tabell 1) och det finns inga systematiska avvikelser mellan modell och data. För att ytterliggare testa den nya modellens egenskaper så simulerade vi den fyra år framåt i tiden, vilket gav oss en modellprediktion på SOFs medlemstal år 2002. Detta upprepades 10 000 ggr och den genererade fördelningen täckte in det observerade medlemstalet 2002, även om modellen i genomsnitt överskattade medlemstalet något.

Diskussion

Antalet medlemmar i SOF styrs av en rad olika faktorer, vilka alla inte kan tas med i en analys som denna. Inte desto mindre visar vår analys att ett antal viktiga lärdomar kan dras ur materialet. För det första är medlemsutvecklingen i SOF skild från befolkningsökningen i Sverige, vilket medför att den positiva medlemsutvecklingen som föreningen haft är en konsekvens av ett generellt ökande intresse för organiserad ornitologi i Sverige, och inte en effekt av en konstant andel intresserade i en ökande befolkning. De senaste 50 åren har en större medvetenhet om naturen och människans påverkan på vår miljö vuxit fram, och det är troligt att det är denna strömning som avspeglas i SOFs medlemstal.

För det andra så finns det under den uppåtgående trenden en antydan till periodicitet i föreningens medlemsantal. En periodicitet som sammanfaller med en ungefärlig generationstid på 20 – 30 år hos oss människor. Detta mönster går inte igen hos SNF, men kan var ett indicium på hur fågelintresset sprider sig över generationsklyftorna. Är det så att ungdomar i hög grad blir inskolade i föreningen av sina föräldrar och att det är detta mönster vi ser i medlemstalen? Kanske är SOF, som är en något snävare förening än SNF, mer påverkad av generationsväxlingar? Det skulle kunna förklara de observerade skillnaderna i medlemsdynamik. I en ideell förening blir enstaka mycket aktiverade personer, s.k. eldsjälar, oerhört viktiga. Några eldsjälar kan under ett antal år bidra till föreningens tillväxt, men det är troligt att de med stigande ålder bidrar mindre och mindre.

Vår modell är onekligen en kraftig förenkling av verkligheten men den har ändå lyckats fånga tillräckligt många av de egenskaper som kännetecknar SOFs medlemsutveckling för att kunna ge rimliga förutsägelser om medlemsantalet år 2002. De mönster som vi har upptäckt i data antyder att förklaringen till skillnaden i SOFs och SNFs populationsdynamik står att finna i hur generationsväxlingarna går till. Det skulle därför vara oerhört spännande att studera dessa övergångar i mer detalj med hjälp av åldersstrukturerade data.

Vad ska då SOF som förening dra för lärdomar av denna analys? Det viktigaste är att se föreningens utpräglade generationstid och att bättre överbrygga växlingen mellan olika generationer. Den senaste svackan skedde under 1960-talet vilket fick Källander & Svensson (1985) att tala om ”den förlorade generationen”. Enligt denna studie så befinner sig SOF ånyo i en generationsväxling och mycket kraft bör därför läggas på att knyta nya ungdomar till föreningen.