

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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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

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

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

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

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

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

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

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 :

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

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 ($\Delta_i = AIC_{ci} - \min AIC_c$) 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 ($\Delta_i = AIC_{ci} - \min AIC_c$) för de alternativa modellerna. N_t = Antal SOF-medlemmar år t , S_t = Sveriges befolkningmängd 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

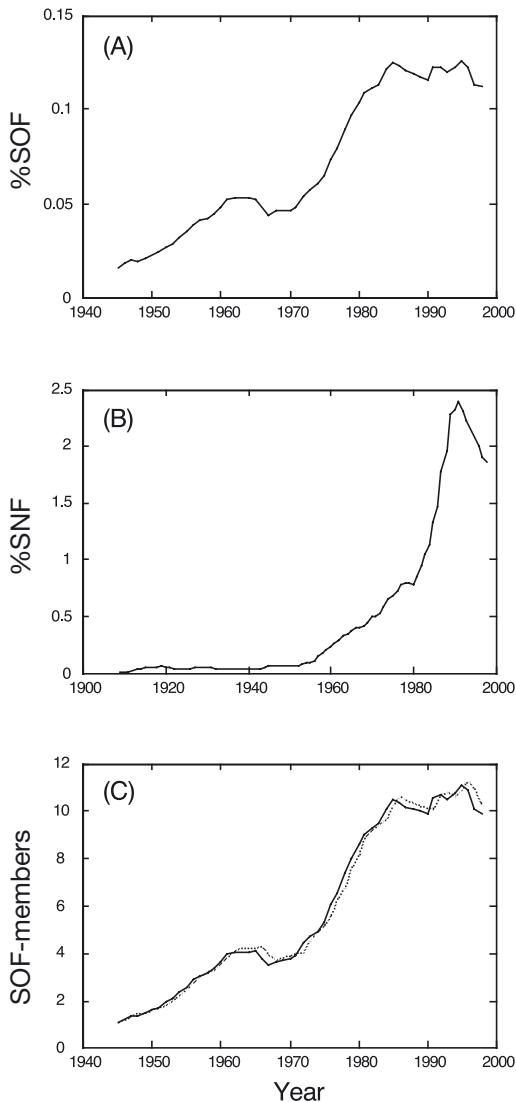


Figure 1. (A–B) The percentage of the Swedish citizens that are members of the Swedish Ornithological Society (SOF) or the Swedish Society for Nature Conservation (SNF). (C) The number of SOF members (solid line) and the best fit of the logistic growth model (dashed line). The point estimates of a and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

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

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

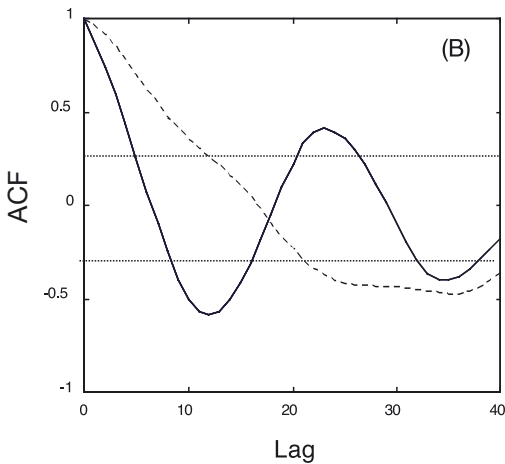
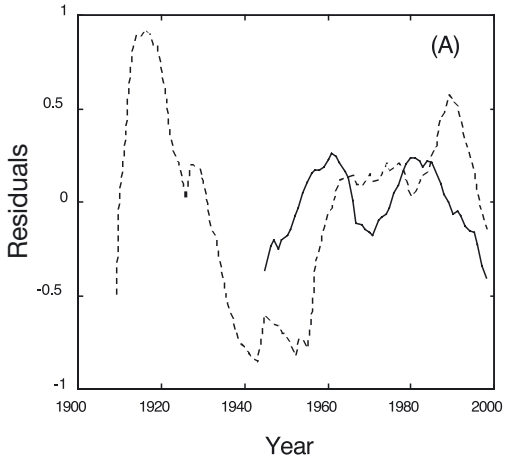


Figure 2. (A) Residual plot after removing a linear trend from the time series of members of the Swedish Ornithological Society (solid line) and the Swedish Society for Nature Conservation (dashed line). (B) Correlogram of the residuals in (A) showing a 23-year cycle in the Swedish Ornithological Society (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). Värderna utanför de streckade linjerna anses vara signifikant skilda från noll.

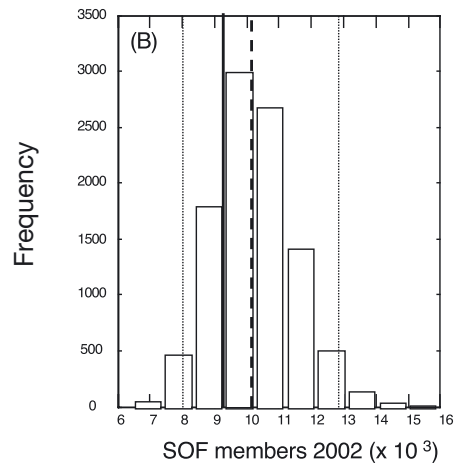
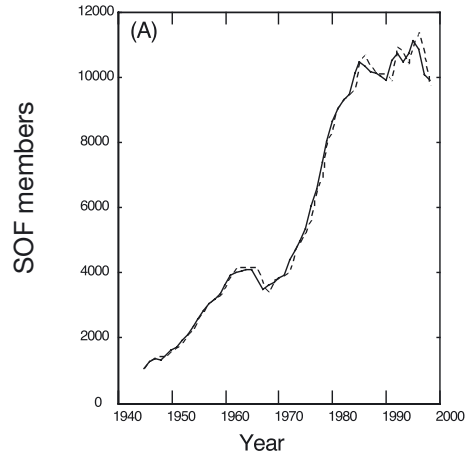


Figure 3. (A) The number of SOF members (solid line) and the best fit of the delayed logistic growth model (dashed line) $N_{t+1} = N_t \exp(a_0 + a_1 N_t + a_2 N_{t-1})$. (B) Histogram showing the predicted number of members in 2002, based on 10,000 iterations of the delayed logistic model. The observed 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) $N_{t+1} = N_t \exp(a_0 + a_1 N_t + a_2 N_{t-1})$. (B) Histogram som visar det predikerade 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 prediktionerna (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

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References

- Alerstam, T. & Hedenström, A. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Burnham, K. P., & Anderson, D. R. 1998. *Model selection: a practical information-theoretic approach*. Springer-Verlag, New York.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation* (2nd ed.). Sinauer Associates, Inc Publishers Sunderland, Massachusetts.
- Chatfield, C. 1999. *The analysis of time series: An introduction* (5th edn). Chapman and Hall, Boca Raton.
- Hilborn, R. & Mangel, M. 1997. *The ecological detective: Confronting models with data*. Princeton University Press, New Jersey.
- Källander, H. & Svensson, S. 1985. Vår fågelvärld – 40 år. *Vår fågelvärld* 40:362–366.
- Nilsson, S. 1858. *Skandinavisk fauna. Foglarna*. Första bandet. Gleerups, Lund.
- Royama, T. 1992. *Analytical population dynamics*. Chapman and Hall, London.
- Svensson, S. 1988. Varför minskar SOF. *Vår fågelvärld* 47:4.
- Svensson, S. 1997. The death of ornithology – Where have all the young ornithologists gone? *Ornis Svecica* 7:175–179. *In Swedish with English summary*.

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 behövs föreningen aktiva medlemmar som verkar för att genomföra föreningens mål. Inom SOF har det under stundom 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 långre 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 fått från föreningens tryckta årsrapport, som jämförelse har även Svenska Naturskyddsföreningens (SNF) medlemsutveckling studerats. Data på Sveriges befolkningssmängd 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 medlemskap 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 SOF's 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 ytterligare testa den nya modellens egenskaper så simulerade vi den fyra år framåt i tiden, vilket gav oss en modellprediktion på SOF's 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 SOF's medlemstal.

För det andra så finns det under den uppåtgående trenden en antydning 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 eldsjälarna 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.

Timing and seasonal changes in Eider *Somateria mollissima* spring migration in the northern Öresund, south Sweden, 1975–2001

MATS PETERZ

Abstract

This paper describes the spring migration of Eiders *Somateria mollissima* through the Öresund, south Sweden, during the years 1975 to 2001. The birds are leaving their wintering grounds in the Kattegat to breed in the Baltic. The passage takes place in the second half of March and the first half of April with the major migration period between 22 March and 13 April (median date 4 April). Over the study years, there is a significant trend that the migration takes place earlier in the season. This is both in terms of median date and

onset of the migration period. The change in the timing of the migration appears to be related to milder winter weather and earlier springs during the end of the 20th century. It is shown that the spring passage of Eiders for individual years is significantly correlated with the ice indices for Swedish seas the preceding winter.

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Introduction

The Eider *Somateria mollissima* is a common bird in many coastal areas of north-western Europe (Cramp & Simmons 1977). A significant part of the population breeds in the Baltic Sea. In the early 1970s this population was estimated at 300,000–350,000 pairs (Almkvist 1974, Alerstam et al. 1974 a). Some ten years later, the Baltic population had increased and was estimated at approx. 400,000 pairs (Koskimies 1993). Out of these, 270,000 pairs bred in Sweden and 130,000–170,000 pairs in Finland.

The main wintering grounds of the Baltic Eider population are located in the south-western Baltic, the Danish straits and in the south-western Kattegat (Figure 1; Durinck et al. 1993, Skov et al. 1995, Fransson & Pettersson 2001). The wintering population in the Kattegat was estimated to be close to 400,000 birds in the mid eighties (Skov et al. 1995). In 1992, 205,000 birds were recorded wintering in the Gulf of Kiel and western Fehmarn Belt between January and March (Durinck et al. 1993). Recoveries of Eiders ringed in Sweden show that the birds are fairly stationary in their wintering grounds

from at least December up to March (Fransson & Pettersson 2001).

In southern Scandinavia the spectacular spring migration of Eiders is taking place during March and April. A detailed combined radar and field study showed that Eiders wintering in the Kattegat are heading mainly in a NE–SE direction (Figure 1) (Alerstam et al. 1974a, b). When the birds reach the west coast of Sweden the majority crosses overland at high altitudes, mostly without being noticed by field observers (Swegen 1972, SOF 2002). To some extent this is because an important part of the Eiders (20 % of registered radar echoes) are migrating during the night (Alerstam et al. 1974a, b). Significant numbers of Eiders are, however, still observed heading south along the Swedish west coast and in the Öresund (Wirdheim 1988, Jönsson et al. 1990), crossing south Sweden at a later stage (Swegen 1972, Alerstam et al. 1974a, b). The majority of Eiders migrating along the south coast of Sweden mostly originate from more southerly wintering grounds, i.e. in the south-western Baltic and the Danish straits (Alerstam et al. 1974a, b).

Although the geographical pattern of the spring migration of Eiders in south Sweden has been

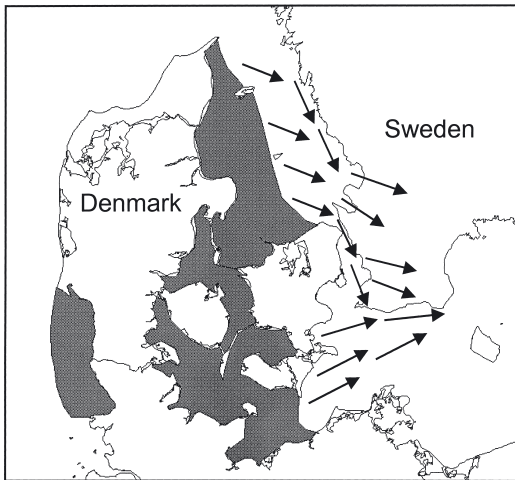


Figure 1. Wintering areas of Eiders *Somateria mollissima* in southern Scandinavia and their principal spring migration pattern over south Sweden.

Ejderns övervintringsområden i södra Skandinavien samt det principiella sträckmönstret över södra Sverige.

described earlier, no detailed analysis of the timing has been published. Here, the seasonal distribution of the Eider spring migration in the northern Öresund, south Sweden, during the years 1975–2001 is described and possible explanations for observed changes in the timing of the passage is discussed.

Materials and methods

This study is based on field observations of the Eider migration in the northern Öresund, along the Swedish coast between Helsingborg and Höganäs during the years 1975 to 2001 (Figure 2). In this area the Öresund is at its narrowest width (approx. 5 km between Sweden and Denmark) and an observer standing at the beach can easily cover the whole southbound migration. Days when more than 1000 Eiders were observed on migration are considered in this study. When observations were carried out at more than one place the same day, only the highest count was taken into account.

Observations of the migration were carried out on a voluntary basis by members of the Ornithological Society of Kullabygden. This means that data were not collected in a strict systematic way. Therefore, to avoid influences of single days with very high numbers of Eiders or differences in observer efforts, statistical analyses are based on number of days with

migration, rather than the actual number of birds counted.

Significant changes in the timing of the migration over the study period were analysed by calculating the Spearman's Rank correlation coefficient (r_s) for the time distribution of days with more than 1000 birds over the years studied. Differences in the timing of the migration between three nine-year periods, respectively, were analysed using Kruskal-Wallis rank sum test.

In this study the major migration period is defined as the period during which 80 % of the birds were observed, i.e. excluding the 10% earliest and 10% latest birds during the migration period. The median date is the day when 50% of the birds have passed.

Results

In total there were reports of 139 days with more than 1000 Eiders migrating south through the northern Öresund during the years 1975–2001. The yearly number of days ranged between 1 and 11, with a median of 5 days per year. The total number of Eiders observed was ca. 790,000. The highest count in one day was 67,800 on 12 April 1986. This year was also highest in the yearly total (90,500 birds) and was followed by 1997 (50,500 birds). In three seasons less than 5000 birds were recorded, but this is probably rather a result of poor reporting or coverage of the Eider migration than a true low yearly total.



Figure 2. Map showing northern Öresund and geographical names mentioned in the text.

Närbild över norra Öresund visande platser nämnda i texten.

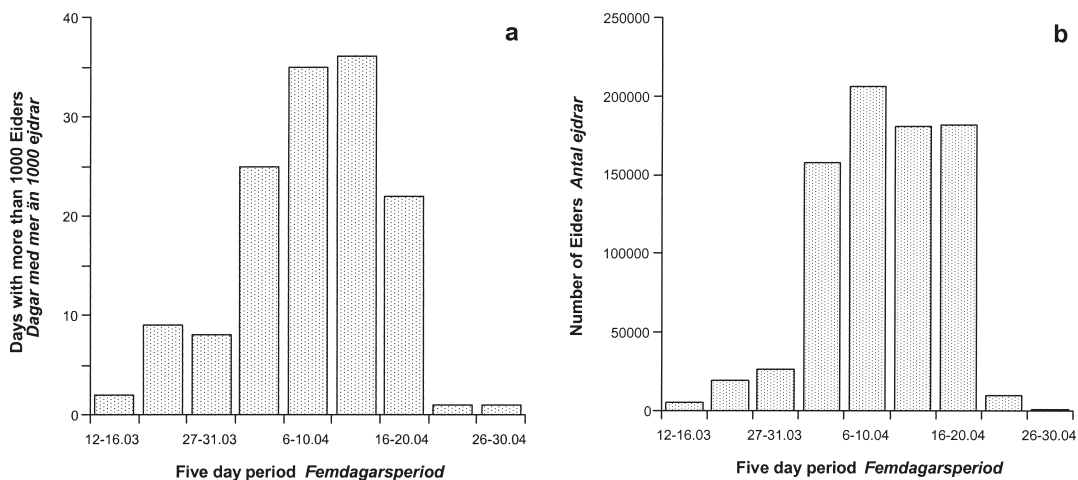


Figure 3. Eider *Somateria mollissima* spring migration in northern Öresund, south Sweden, grouped into five-day periods (Berthold 1973). a: Number of days with more than 1000 birds, b: Number of birds.

Ejdersträckets tidsmässiga förlopp i norra Öresund, fördelat på femdagarsperioder (Berthold 1973). a: antal dagar med mer än 1000 fåglar; b: antal fåglar.

The migration of Eiders in the northern Öresund peaks in the beginning of April (Figure 3a and 3b). The earliest date with more than 1000 birds was on 15 March 1998 and the latest on 22 April 1979. Based on number of days with more than 1000 birds on migration, the major migration period falls between 22 March and 13 April (Table 1) and the median date on 4 April. If instead the actual number of birds observed are considered, the major migration period falls between 28 March and 13 April, with the median date on 5 April.

The seasonal timing of the Eider spring migration has changed during the years covered in this study. Looking at the full data set there is a significant trend that days with more than 1000 migrating Eiders fall earlier ($r_s = -0.357$, $n = 139$, $p < 0.001$) in the season towards the end of the analysed time period (Figure 4).

When grouping the data into three nine-year periods it can be seen that the median migration date during the latest period, 1993–2001, falls 5 days earlier ($\chi^2 = 17.8$, $p < 0.001$) than during the two preceding periods 1975–1983 and 1984–1992 (Table 1). In addition, there is also a trend that migration is initiated and terminated earlier in recent years. A test looking at the relation between the earliest and latest day with more than 1000 migrating birds each year (only years with at least three days of migration

reported are included) shows a significant correlation with the earliest day ($r_s = -0.549$, $n = 22$, $p < 0.01$) but not with the latest ($r_s = -0.124$, $n = 22$, $p > 0.05$).

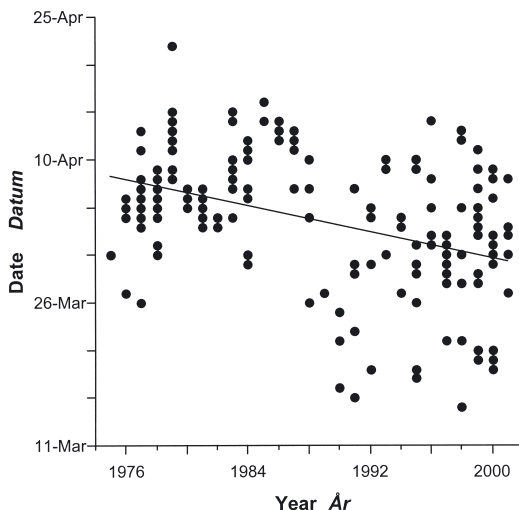


Figure 4. Days with more than 1000 Eiders *Somateria mollissima* on spring migration in northern Öresund, south Sweden, during different years.

Dagar med mer än 1000 ejdrar på vårsträck i norra Öresund under olika år.

Table 1. Earliest and latest record, major migration period (P 10%–P 90%), and median date of days with more than 1000 Eiders *Somateria mollissima* on spring migration in northern Öresund, south Sweden, during different years *Tidigaste och senaste observation, huvudsträckperiod (P 10%–P 90%) och mediantdatum för dagar med mer än 1000 ejder på vårsträck i norra Öresund under olika år*

Years	Days	Earliest	P ₁₀	Median	P ₉₀	Latest
År	Dagar	Tidigaste	P ₁₀	Median	P ₉₀	Senaste
1975–1983	47	26 Mar	1 Apr	6 Apr	14 Apr	22 Apr
1984–1992	33	16 Mar	20 Mar	6 Apr	14 Apr	16 Apr
1993–2001	59	15 Mar	20 Mar	1 Apr	10 Apr	14 Apr
All Alla	139	15 Mar	22 Mar	4 Apr	13 Apr	22 Apr

Discussion

This study shows that the spring migration of Eiders wintering in the Kattegat is now taking place earlier than some twenty years ago. There may be several reasons for this change and in the following, I will discuss two possible alternatives.

Population increase

During the last decades of the 20th century the Baltic Eider population has increased considerably (Roos 1978, 2001, Stjernberg 1982, Koskimies 1993, Lyngs 2000). When a population is growing, competition for breeding grounds will increase and it will be advantageous to arrive early in the breeding season to occupy the most favourable territories. In this case an early initiation of the migration would enable early arrival to the breeding grounds and could explain the observed change in the timing of the migration period.

Climate changes

Earlier studies have shown that that warm, westerly winds coincide with high intensity in the Eider migration both in the Kattegat (Alerstam et al. 1974a, b, Karlsson 1976, Malling Olsen 1992) and in the Baltic (Pettersson 1981). Therefore, the seasonal change in the migration period could also be a response to recent climate changes with milder winters and earlier springs (SMHI 1999). A reasonable indicator of winter severity and spring arrival is the ice indices of Swedish seas as calculated by SMHI (1999). Comparison of the time distribution of days with Eider migration in the northern Öresund

each spring and the ice indices the preceding winter (Figure 5) shows that these are significantly correlated ($r_s = -0.515$, $n = 134$, $p < 0.001$). This indicates that climate change has had an influence on the timing of migration.

The Eider migration through the Kalmarsund, south-east Sweden, was extensively studied during the years 1963–1972 (Pettersson 1981). Based on data presented by Pettersson (1981), the median date

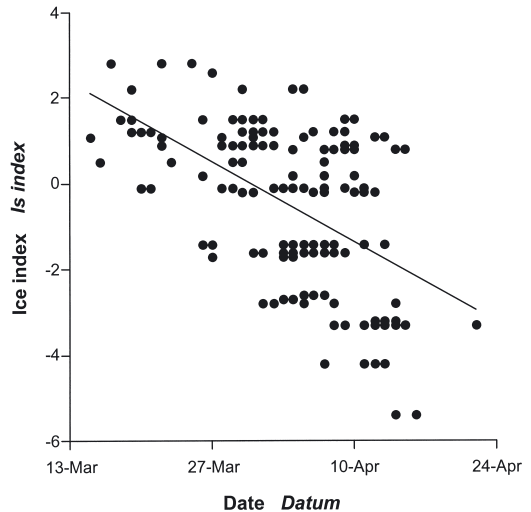


Figure 5. Relation between days with more than 1000 Eiders *Somateria mollissima* on spring migration in northern Öresund, south Sweden, and the ice indices of Swedish seas the preceding winter.

Förhållandet mellan dagar med mer än 1000 ejdrar på vårsträck i norra Öresund och föregående vinters is-index i svenska farvatten.

can be estimated to fall on 11 April, which is five days later than in the northern Öresund during the years 1975–1983 (Table 1). Although it is reasonable to assume that the migration takes place earlier closer to the wintering grounds, the difference between median dates is surprisingly large. The distance between the Kattegat and the Baltic, across land, is around 250 km and with a flight speed of approx. 70 km/h (Rydén & Källander 1964), Eiders would reach the southern Baltic within a few hours depending on wind conditions. This is supported by field observations showing that days with Eider peak migration often coincide at several observation spots in south Sweden (Blomdahl et al. 2001, Elleström et al. 2002).

Looking at the ice indices for the years covered in the Kalmarsund study, the winters during this period were overall colder than normal and there were also several winters with severe, or very severe, ice situations (SMHI 1999). Thus the timing of the Eider migration in Kalmarsund also seems to correlate well with the ice indices, which supports the explanation that the earlier migration in recent years is primarily a reflection of climate changes, i.e. milder winters and earlier springs.

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References

Alerstam, T., Bauer, C.-A., & Roos, G. 1974a. Spring migration of Eiders *Somateria mollissima* in Southern Scandinavia. *Ibis* 116: 194–210.

Alerstam, T., Bauer, C.-A., & Roos, G. 1974b. Fält- och radarstudier av östersjöejdrarnas *Somateria mollissima* vårsträck. *Vår Fågelvärld* 33: 15–27.

Almkvist, B., Andersson, Å., Jogi, A., Pirkola, M. K. Soikkeli, M & Virtanen, J. 1974. The number of adult Eiders in the Baltic. *Wildfowl* 25: 89–94.

Berthold, P. 1973. Proposals for the standardization of the presentation of data of annual events, especially migration data. *Auspicium* 5, Suppl. 49–57.

Blomdahl, A., Elleström, O., Johansson, B. & Skyllberg, U. 2001. Sjöfågelsträcket 2000. In: SOF 2001. *Fågelåret 2000*. Stockholm.

Cramp, S. & Simmons, K.E.L. (eds.) 1977. *The Birds of the Western Palearctic*, Vol. I. Oxford University Press.

Durinck, J, Skov, H. & Andell, P. 1993. Seabird distribution and numbers in selected offshore parts of the Baltic Sea,

winter 1992. *Ornis Svecica* 3: 11–26.

Elleström, O., Johansson, B. & Skyllberg, U. 2002. Sjöfågelsträcket 2001. In: SOF 2002. *Fågelåret 2001*. Stockholm.

Fransson, T. & Pettersson, J. 2001. *Svensk ringmärkningsatlas*. Vol. 1. Stockholm.

Jönsson, P. E., Nilsson, K. G., Oldén, B., Peterz, M. & Strid, C. 1990. *Nordvästskånska Fåglar*. Helsingborg.

Karlsson, J. 1976. Flyghöjden hos ejder under värflyttningen över sydligaste Skåne – bestämning med hjälp av radar. *Fauna och Flora* 71: 151–157.

Koskimies, P. 1993. *Population sizes and recent trends of breeding birds in the nordic countries*. Helsinki.

Laursen, K. 1989. Estimates of sea duck winter populations of the Western Palearctic. *Danish Rev. Game Biol.* 13: 6: 1–22.

Lyngs, P. 2000. Status of the Danish breeding population of Eiders *Somateria mollissima* 1988–93. *Dansk Orn. Foren. Tidsskr.* 94: 12–18.

Malling Olsen, K. 1992. *Danmarks Fugle – en oversigt*. Dansk Ornitologisk Forening.

Pettersson, J. 1981. Ejderens *Somateria mollissima* vår- och höststräck längs Ölands kuster. *Proc. Second Nordic Congr. Ornithol.* 1979. Norsk Ornitologisk Forening, Stavanger.

Roos, G. 1978. Sträckräkningar och miljöövervakning: långsiktiga förändringar i höststräckets numerär vid Falsterbo 1942–1977. *Anser* 17: 133–138.

Roos, G. 2001. Sträckfågelräkningar vid Falsterbo 2000. I: SkOF. *Fåglar i Skåne 2000*. Lund, pp. 77–90.

Rydén, O. & Källander, H. 1964. Beräkning av ejderens (*Somateria mollissima*) sträckhastighet. *Vår Fågelvärld* 23: 151–158.

Skov, H., Durinck, J., Leopold, M.F. & Tasker, M.L. 1995. *Important Bird areas for seabirds in the North Sea*. Birdlife International, Cambridge.

SMHI. 1999. *Väder och vatten under ett århundrade 1900–1999*.

SOF. 2002. *Sveriges Fåglar*. 3:e uppl. Stockholm.

Stjernberg, T. 1982. The size of the breeding Eider population of the Baltic in the early 1980s. *Ornis Fennica* 59: 135–140.

Swegen, H. 1972. Ejderens *Somateria mollissima* sträck över land i södra Sverige. *Vår Fågelvärld* 31: 183–190.

Wirdheim, A. 1988. Vårsträcket av sjöfåglar i Laholmsbukten. *Fåglar i södra Halland* 1987: 11–30.

Sammanfattning

Tidpunkt och säsongsförändring för vårsträcket av ejder Somateria mollissima i norra Öresund, södra Sverige, 1975–2001

En betydande del av det europeiska ejderbeståndet häckar i Östersjön. Den totala populationen här har uppskattats till ca 400.000 par (Koskimies 1993). Östersjöejdrarna har sina viktigaste övervintringsområden i sydvästra Östersjön, i Bälten samt längs den danska Kattegattkusten (Figur 1). Man har beräknat att ungefär 400.000 ejdrar övervintrar i Kattegatt (Skov et al. 1995). I mars–april sträcker dessa mot NE–SE till sina häckplatser i Östersjön (Figur 1). Kombinerade radar- och fältstudier har visat att

ejdrarna när de når den svenska västkusten till stor del sträcker in över land på hög höjd utom synhåll från marken (Swegen 1972, Alerstam et al. 1974a, b). Betydande antal ejdrar sträcker emellertid även söderut längs Västkusten och genom Öresund (Jönsson et al. 1990, Wirdheim 1988) för att korsa Sydsvrige längre söderut (Swegen 1972, Alerstam et al. 1974a, b). Majoriteten av de ejdrar som på våren ses sträcka längs Skånes sydkust härstammar från övervintringsplatser i sydvästra Östersjön och i de danska Bälten (Alerstam et al. 1974a, b).

Även om ejdersträckets geografiska mönster i södra Sverige är välbeskrivet har inte mycket publicerats om dess tidsmässiga förlopp. Baserat på fältobservationer under åren 1975–2001 beskrivs här ejderns vårflyttning genom norra Öresund, särskilt med avseende på dess tidsmässiga förlopp samt på de förändringar som skett under senare år.

Material och metoder

Denna sammanställning bygger på observationer av sydsträckande ejdrar i norra Öresund längs kuststräckan mellan Helsingborg och Höganäs (Figur 2). Dagar med minst 1000 observerade ejdrar under åren 1975–2001 har tagits med i studien. Om observationer skett på flera platser samtidigt har endast det högst registrerade antalet beaktats.

Observationerna har utförts av medlemmar i Kullabygdens Ornitologiska Förening på frivillig basis, vilket medfört att data inte samlats in på ett strikt systematiskt sätt. För att undvika att enstaka dagar med många sträckare eller olikheter i observationstid skall påverka resultatet av denna studie, baseras statistiska analyser på antal dagar med minst 1000 flyttande ejdrar, istället för antal inräknade fåglar.

Trender under de behandlade åren har analyserats med hjälp av Spearman's Rank korrelation (r_s). Skillnader i sträcket tidsmässiga förlopp under tre nioårsperioder 1975–1983, 1984–1992 and 1993–2001 har undersökts med Kruskal-Wallis ranksumme-test.

I analysen definieras huvudsträckperioden som den period under vilken 80% av fåglarna observerats, d.v.s. de tidigaste resp. senaste 10 % av sträckarna har utslutits. Mediandatum är den dag då 50% av fåglarna har passerat.

Resultat

Under åren 1975 till 2001 räknades mer än 1000 sträckande ejdrar per dag i norra Öresund vid 139

tillfällen. Antalet rapporterade dagar per år varierar mellan 1 och 11. Det totala antalet räknade ejdrar uppgick till ca 790.000. Högsta dagssiffra var 67.800 den 12 april 1986. Samma år noterades även den högsta årssumman (90.500) följt av 1997 (50.500). Tre vårar rapporterades färre än 5000 ejdrar totalt, men detta beror snarare på bristande rapportering eller bevakning än att sträcket var dåligt dessa år.

Ejderns vårsträck i norra Öresund kulminerar första halvan av april (Figur 3a och 3b). Tidigaste observationsdag med mer än 1000 sträckande ejdrar inföll 15 mars 1998 och senaste 22 april 1979. Tittar man på dagar med minst 1000 ejdrar inföll huvudsträckperioden mellan 22 mars och 3 april (Tabell 1) med mediandatum 4 april. Om man istället tittar på antalet fåglar infaller huvudsträckperioden mellan 28 mars och 13 april, med mediandatum 5 april.

Ejdersträckets tidsmässiga förlopp har förändrats under den studerade tidsperioden. Det föreligger en signifikant trend att dagar med mer än 1000 sträckande ejdrar inträffar allt tidigare på våren (Figur 4, $r_s = -0.357$, $n = 139$, $p < 0.001$). Om materialet grupperas i tre nioårsperioder kan man konstatera att mediandatum infaller fem dagar tidigare under åren 1993–2001 (Kruskal-Wallis ranksummetest, $\chi^2 = 17.8$, $p < 0.001$), jämfört med de två tidigare perioderna (Tabell 1). Även inledningen av vårsträcket sker tidigare ($r_s = -0.549$, $n = 22$, $p < 0.01$). Däremot ser man ingen sådan trend när det gäller sträckperiodens avslutning ($r_s = -0.124$, $n = 22$, $p > 0.05$).

Diskussion

Denna studie visar att vårflyttningen hos ejdrar övervintrande i Kattegatt sker tidigare under säsongen numera än för ett tjugotal år sedan. Det kan finnas flera förklaringar till detta av vilka två diskuteras i det följande.

Under senare delen av 1900-talet har den häckande ejderpopulationen i Östersjön ökat markant (Roos 1978, 2001, Stjernberg 1982, Koskimies 1993, Lyngs 2000). I en växande population kommer konkurrensen om häckplatser att öka. Det är då en fördel att anlända tidigt på våren och lägga beslag på de bästa reviren, vilket i så fall skulle kunna förklara varför vårsträcket sker tidigare numera.

En viktig sträckutlösande faktor för ejdern är västliga vindar i kombination med varmluftsinnbrott (Alerstam et al. 1974a, b, Karlsson 1976, Malling Olsen 1992, Pettersson 1981). Därför skulle en annan förklaring till det tidigare ejdersträcket kunna vara

de senare årens klimatförändringar med allt mildare vintrar och tidigare vårar (SMHI 1999). En indikator på den kombinerade effekten av vinterväder och vårens meteorologiska ankomst är det is-index som beräknats för svenska färsvatten (SMHI 1999). När detta jämförs med ejdersträckets tidsmässiga förlopp den efterföljande våren (Figur 5) finns ett signifikant samband ($r_s = -0.515$, $n = 134$, $p < 0.001$), vilket

indikerar att klimatförändringar kan förklara de observerade förändringarna. Detta antagande stöds även av studier av ejdersträcket i Kalmarsund åren 1963–1972 (Pettersson 1981). Enligt SMHIs is-index var flertalet vintrar under denna period stränga eller mycket stränga samtidigt som sträckets mediandatum inföll 11 april, d.v.s. betydligt senare än vad som var fallet i denna studie.

Birds in the cold: The effects of plumage structure and environment on operative temperature, shown by spherical models

FLIP STOUTJESDIJK

Abstract

What is the maximum insulating effect the available plumage of a bird can provide? To address this question I photographed free-living birds in such a way that the total volume of the bird could be estimated. It was then assumed that the bird could be represented by a sphere of the measured volume with a core (kept at 40 °C) of which the volume in cm³ was equal to the bird's mass in g. The overall thermal conductance of the spherical model was calculated and compared with what could be expected for real birds based on metabolic data from the literature. The conductance calculated for the models was consistently lower than predictions from the literature. The discrepancy was as could be expected, and became smaller with decreasing size. For small

birds the fit was quite good and the relative plumage thickness approached the value where further increase would have a relatively small effect. The model suggests that the operative temperature of a small bird perching in the sun on a cold winter day can exceed the air temperature by more than 20 °C on thermally favoured sites. Alternatively expressed, the energy saved can exceed the basal metabolic rate. For a plumage penetrable for solar radiation the excess may be still higher, even when the reflectivity is rather high. It is estimated that the operative temperature may exceed the preferred range already with an air temperature of 10 °C.

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Introduction

About a century ago it was established that also for a living animal the first law of thermodynamics holds which means that the incoming flows must match the outgoing ones. Thus, the question in bird energetics is not whether the energy loss is balanced by energy gains but rather how the birds manage to make them meet.

For a bird in the winter, the thickness of its coat, that is the degree of insulation, is not the only question, perhaps not even the most important one. To maintain its often large temperature difference with the surroundings, it must burn fuel which must be collected as food or taken from an energy reserve. Furthermore, the living tissue might quite well be limited in its capacity to produce heat even when there is plenty of fuel. The heat loss, per unit surface, of e.g. a Willow Tit *Parus montanus* can be of the same magnitude as that of a well dressed human in the winter (see Appendix), but the latter has about 25 times as much living tissue, again per unit surface, to provide the requisite heating power.

I concentrate here on the process of heat loss to the environment. The first step in the heat transport from the core of a bird to the environment is conduction, initially from the internal parts of the body to the skin and then through the plumage to the outer surface. The second step is the transfer of this heat to the surroundings. There is a direct transfer of heat from the surface to the air where it is carried off by convection currents. The convection process depends on the temperature difference between surface and air, the airflow, and the size of the bird or, as in this study, an object that mimics a bird. Parallel with the convection process there is a transfer of heat by radiation which is both emitted and received by the surface. Finally there is solar radiation that is absorbed or reflected but not emitted by the surface.

The purpose of the paper is in the first place to explore how far a simple physical model can take us to understand the thermal situation of a bird in the winter. When a little bird during a cold winter day perches with its feathers fluffed it can be seen as 'a ball of feathers' of almost spherical shape. It is

logical to assume that the spherical shape has to do with minimizing heat loss. It is, however, interesting to take a closer look at the quantitative side of the matter.

One can ask: what size is such a ball and how much living bird tissue is there inside it? I will investigate if it is possible to make an acceptable thermal model of a bird in the winter by considering its body as a sphere kept at a temperature of ca. 40 °C and surrounded by a concentric sphere of insulating feathers. The heat loss of such an object can be readily calculated in relation to environmental factors on the one hand and its dimensions and thermal properties on the other hand.

By means of photographs I estimated the volume of birds under winter conditions and then calculated the heat loss of a spherical model of the same volume, with a core kept at 40 °C, i.e. a model which imitated the thermal properties of the living bird as far as possible. Finally these data were compared with literature data on heat loss from living birds derived from metabolic measurements under laboratory and field conditions. Furthermore, I asked the question to what extent a bird can make use of the solar energy both by selecting its position in relation to sunshine, shade, or reflecting surfaces, and by structuring its plumage.

I gave special attention to small northern forest birds since they experience an especially demanding thermal and radiative environment. I could show the important result that by means of simple physical and theoretical models it is possible to understand how sunshine can mitigate the effect of a low air temperature or cause heat stress already at moderate but still fairly low air temperatures.

Materials and methods

The volume of a range of free-living birds was estimated by photographing them in profile side by side with a sphere of known size. Alternatively, a calibration picture of the sphere was taken immediately after the bird had been photographed with an unchanged setting of the lens. The pictures were taken of active birds during short intervals of rest, in the shadow, with air temperatures of -5 to -25 °C, mainly in southern Sweden but occasionally at Abisko in northern Sweden and in the Netherlands. From the photographs I estimated the volume of the birds by considering them to be ellipsoid or egg-shaped bodies since birds are shaped like elongated round bodies rather than perfectly round balls. The volume of such bodies that "revolve" around a

central axis can be calculated by "cutting" them into series of circular discs. Focal lengths of 30 and 56 cm were used to obtain sharp pictures of sufficient size to permit good estimates of the volume.

I assumed that the volume of a bird without plumage in cm³ is the same as its mass with feathers in g, a plausible approximation as the density of a 'naked' bird is somewhat below 1 (Schmidt-Nielsen 1972). From these data I calculated the dimensions of spherical, theoretical models that I used as thermal models of the birds. These models consisted of an inner spherical core surrounded by a concentric insulating layer. For example, a Great Tit *Parus major* that has a total volume of 90 cm³ and a mass of 18 g was represented by a hypothetical sphere with total volume of 90 cm³ and an outer radius, r_o , of 2.78 cm. The spherical core would then have a volume of 18 cm³, giving an inner radius, r_i , of 1.63 cm. The thermal conductance of the model was then calculated and compared with literature data for a real tit, based on metabolic measurements. Average mass of the birds was taken from Snow & Perrins (1998). The thermal models can be seen as links between real birds and the temperature measurements in the experimental bulbs with the only purpose of making accurate calculations possible.

The heat loss of such a spherical core of uniform temperature, t_b , depends on the thermal conductivity of the insulation, on r_i and r_o as well as on wind, air temperature t_a , and radiation (cf. Stoutjesdijk & Barkman 1992). The heat loss in Watts, M , can be expressed as

$$M = C_0 (t_b - t_a)$$

for situations where thermal or solar radiation need not be considered, as in dense forest or under laboratory conditions. Here C_0 is the overall thermal conductance. The effect of radiation can be included by replacing t_a by an effective or operative temperature t_e . For living birds the term "operative temperature" is commonly used (Bakken 1976, 1992) whereas I use the term "effective temperature" for the models. These terms have a long history in medical physiology. They aim to describe a complicated thermal environment by a single temperature that easily can be measured (Evans 1945, Fanger 1972, Gonzales et al. 1974). In the following I make clear that the temperature of a simple model such as a black bulb will have a close relationship to the operative temperature of a bird.

Extensive series of measurements of the overall conductance can be found in the literature (Kendeigh et al. 1977). These were used for comparison with

the thermal models that were calculated from the photographs. The overall conductance of the models was calculated for the laboratory conditions to which most data on living birds refer. I also estimated how the models would behave under more realistic environmental conditions, in the first place how much the effective temperature in the sun could exceed air temperature.

For this purpose I measured solar radiation (Kipp Solarimeter), thermal radiation (Stoutjesdijk & Barkman 1992) and temperatures in experimental models that I constructed (Stoutjesdijk, 2002). The models were of two types: dull black bulb-shaped ones that minimize reflection and "fluffy" models that mimic the properties of real birds. These experimental models were the most important part of the instrumentation. They were made of aluminium cake forms with a wall thickness of 0.06 mm and equipped with a temperature sensor in the centre. The temperatures were measured with simple outdoor digital thermometers that were calibrated with an accurate mercury thermometer.

The black bulbs consisted of single-layered half-spheres that were glued together and painted with dull black paint. The fluffy models consisted of two concentric spheres with a layer of insulating down or fibres in between. I made two sizes of this fluffy model; a smaller one with an inner diameter of 3.0 cm and an outer diameter of 5.8 cm and a larger one with twice these dimensions. A segment that covered approximately 20% of the total surface, was removed from the outer sphere (cf. Figure 3d). Such a sphere can be considered to thermally mimic a bird with a plumage that is partially penetrable for solar radiation. The small models were made both with eider down (reflectivity ca. 20%) and with white artificial fibre (reflectivity ca. 57%) whereas the large one was made with eider down only. These models were black apart from the fluffy section resulting in a reflectivity of around 57% and 20% for approximately 20% of the surface, and a low reflectivity from the rest of the surface. In total I thus made four thermal models, one black bulb, two smaller and one larger fluffy model.

Results

I constructed a nomogram (Figure 1) that shows the relation between mass and overall thermal conductance (C_o) for models with a range of values of the quotient between the outer and inner radii, r_o/r_i , between 1.2 and 2.0. On a double logarithmic scale this results in a series of almost straight lines.

The calculations were made for still air and a specific conductivity of the plumage of 0.04 W/m °C. This is conservative since this is equal to the best insulators both in the animal world and among man-made materials (Scholander et al. 1950, Taylor 1986). The values of the r_o/r_i -quotient derived from the photographs were placed on their proper place in the nomogram and thus the expected overall conductance could be read.

In the nomogram the regression lines for passerines and non-passerines give the relation between mass and overall conductance, C_o , according to Kendeigh et al. (1977). Here the overall thermal conductance was derived from the metabolic heat production, i.e. oxygen consumption of birds under laboratory conditions. These measurements were made in still air with a temperature of 0 °C, which makes them comparable with those given here.

To place the data on the thermal properties of birds in an environmental context I here present calculations of the effective temperatures of spherical models. These estimates are based on measurements of air and surface temperature, solar and thermal radiation and temperatures of both the black bulbs and the fluffy models. The diameter of the bulbs was 5.8 cm when not stated otherwise. Where the physical aspects of the data per se need some explanation I give it here and for the rest I refer to the discussion.

The temperatures of the bulbs indicate how the radiation affects the operative temperature of a bird. Figure 2 shows the effective temperatures for theoretical models with the thermal properties of a "standard thermal model" corresponding to a 12 g bird. The heating power that would be required to keep such thermal models at 40 °C is expressed in units of the basal metabolic rate (BMR) of the standard model (see Figure 3 and discussion). The diameter of the standard thermal model was almost the same as the black bulb meaning that its effective temperature was equal to the black bulb temperature (see Appendix). The data in Figure 2 are based on measurements of radiation conditions and black bulb temperatures on two calm and cloudless winter days. The first set of measurements was made with a solar elevation of 10° by the end of December at noon in southern Sweden. The air was completely still, not even in the treetops there was a sign of air movement. The black bulb temperature was twelve degrees above air temperature (-5 °C) giving an effective temperature of +7 °C and the requisite heating power 1.74 B.M.R for a black standard model.

For a model (or bird) that is not black the effective

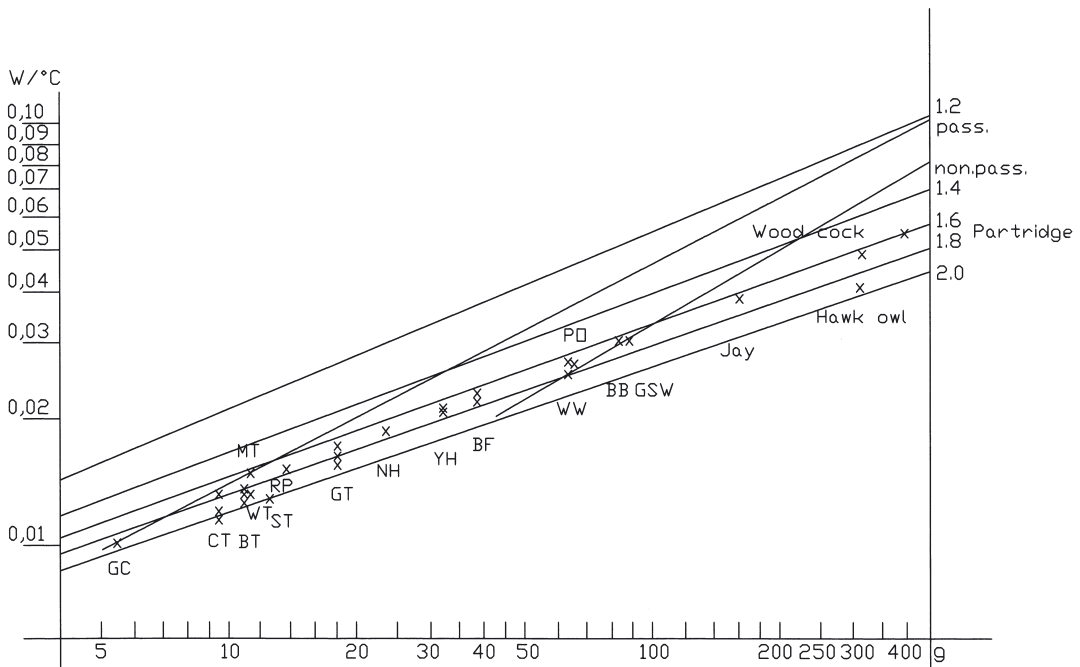


Figure 1. Nomogram showing the relation between overall thermal conductance (Y-axis, left) and mass (X-axis). It is supposed that the core volume in cm^3 is equal to the mass in g. The five almost parallel lines: thermal models with plumage thickness (r_u/r_r) between 1.2 and 2.0 (Y-axis, right). The two crossing lines: passerines and non-passerines; data from the literature. The relative coat thickness for free-living birds, derived from photographs, is shown by (x) in the diagram. The abbreviations refer to the list of species below.

De fem nästan parallella linjerna ger relationen mellan kärnvolumen (cm^3) och total termisk konduktans (C_0) för teoretiska sfäriska modeller med relativfjäderdräktstjocklek (r_u/r_r) mellan 1.2 och 2.0. Värden av r_u/r_r för fåglar: x. De två korsande linjerna visar relationen mellan vikt (i gram) och C_0 för tättingar och icke-tättingar från litteraturvärden.

List of the bird species *Lista över fågelarterna:*

GC, Goldcrest, *Kungsfågel*, *Regulus regulus*. CT, Coal Tit, *Svartmes*, *Parus ater*. BT, Blue Tit, *Blåmes*, *Parus caeruleus*. MT, Marsh Tit, *Entita*, *Parus palustris*. WT, Willow Tit, *Talltita*, *Parus montanus*. ST, Siberian Tit, *Lappmes*, *Parus cinctus*. RP, Redpoll, *Gråsiska*, *Carduelis flammea*. GT, Great Tit, *Talgöxe*, *Parus major*. NH, Nuthatch, *Nötväcka*, *Sitta europaea*. YH, Yellowhammer, *Gulspary*, *Emberiza citrinella*. BF, Bullfinch, *Domherre*, *Pyrrhula pyrrhula*. WW, Waxwing, *Sidensvans*, *Bombycilla garrulus*. PO, Pygmy Owl, *Sparvuggla*, *Glauclidium passerinum*. BB, Blackbird, *Koltrast*, *Turdus merula*. GSW, Great Spotted Woodpecker, *Större hackspett*, *Dencrocopos major*. Jay, *Nötskrika*, *Garrulus glandarius*. Hawk Owl, *Hökuggla*, *Surnia ulula*. Partridge, *Rapphöna*, *Perdix perdix*.

temperature is of course lower when the surface is impenetrable for solar radiation. In Figure 2 the calculated effective temperatures are shown for theoretical spherical models of which the 20% of the surface that is penetrable to solar radiation has a reflectivity of 50% and the rest a reflectivity of 20%. A model of this kind will mimic a real bird such as a Willow Tit with fluffed breast feathers much better if the most reflective part of the insulation is assumed to be penetrable to solar radiation. In this case the radiation can be much more effective than if it is absorbed at the surface (Walsberg et al. 1978, Stoutjesdijk 2002). When the fluffy models are

directed so that their fluffed breast feathers face the sun their calculated effective temperature exceeds the black bulb temperature. The calculated effects were of medium strength when compared with the results obtained experimentally on various penetrable coats (see Figure 4, Table 1, and Stoutjesdijk 2002). The solar radiation can also be more effective, that is the operative temperature higher, when the plumage on the side facing the sun is thinner or of a higher conductance than on the "shadow" side (cf. Figure 3 and Appendix).

Up to now I have considered only freely exposed probes. Again starting from experiments with black

bulbs and radiation measurements, the calculated temperature of all the three models was found to be considerably higher close to, or almost touching, the densely needled branches of a Juniper or a spruce facing the sun (Figure 2). This happens because the diffuse solar radiation from the transparent blue northern sky is replaced by the stronger reflected radiation from the needles. Furthermore the probes receive long-wave (heat) radiation from the needles instead of the sky. The latter, when cloudless, can be considered as a dome with a temperature as low as 40 °C below air temperature, whereas the needles have a temperature up to 8 °C above air temperature (Stoutjesdijk 1977, Stoutjesdijk & Barkman 1992). A minor effect may also be the somewhat higher (1–2 °C) air temperatures close to the branches. Altogether the effective temperatures of the three models can be further enhanced several degrees (4–6 °C, see legends Figure 2, elevation 10°, right side) by choosing the right position, always considering situations within the possibilities of a small bird.

Due to the low radiation intensity on a horizontal plane (global radiation) the effect of reflected radiation was rather small here, in spite of the fact that scattered snow patches gave a surface reflectivity of 41%. Where there is much reflected radiation from a south oriented snow-covered slope, the temperature excess for a black bulb may be over 20 °C with the same solar elevation.

With a higher solar elevation (30°) the direct solar beam is stronger because of the shorter path through the atmosphere. Also the reflected radiation is more important, even though the reflectivity (albedo) was less (20%), as the radiation intensity on a horizontal plane increases strongly with elevation.

The black bulb temperature was 18 °C above air temperature. The measured radiation conditions and black bulb temperature were also used to construct Figure 3. The radiation fluxes were averaged over a sphere, and together with the black bulb temperature they were used to calculate, for the three thermal models in two positions, the temperature when passive and the heating power needed to keep the core temperature at 40 °C with an air temperature of 0 °C.

Figure 4 shows a synoptic picture of radiative conditions and the temperatures of various types of physical models on a clear still winter day with a solar elevation of 20 degrees and a closed snow cover. The black bulb attained a temperature of 21 °C over air temperature. The partially penetrable ('fluffy') model of the same size showed a temperature excess (Δt) of 31 °C, and the larger fluffy model showed a Δt of 42 °C. On the sunny side of a large

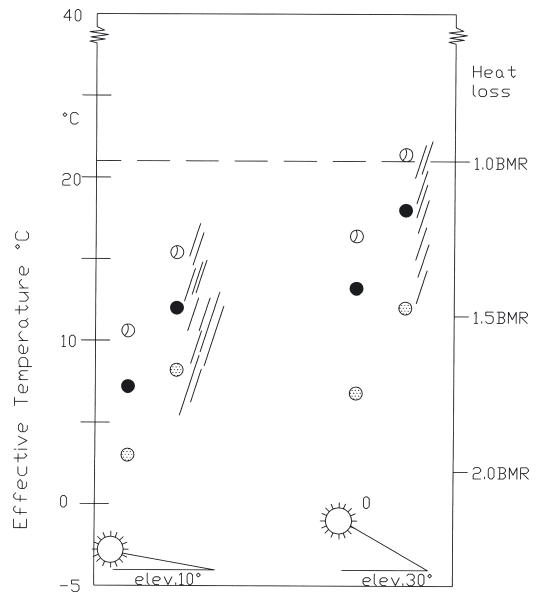


Figure 2. Operative (= effective) temperatures and heat loss for Standard Models with a relative coat thickness (r_u/r_l) of 1.88 that represents a small Passerine of 12 g. The basal metabolic rate (BMR) is used as the unit of heat loss (see text). Air temperature: -5 °C. The calculations are based on measurements of radiation and black bulb temperatures in still air, a cloudless sky and solar elevations of 10° and 30°. The symbols ● and ○ denote the black and fluffy bulbs respectively. For the fluffy model the segment with 50% reflectivity is facing the sun and the solar radiation penetrates the coat to an average depth of 25% of the coat thickness. The symbol ⊙ gives the average effective temperature when the latter model is impenetrable and in a random position. For both solar elevations the data refer to a freely exposed model (left) and one close to dense south-exposed, spruce or Juniper branches.

Operativa (= effektiva) temperaturer (till vänster) och värmeförlust (till höger) för standardmodeller som representerar en tätting på 12 g, vars basalmetabolism har använts som enhet för värmeförlust. Lufttemperaturen är -5 °C. Beräkningarna baseras på mätningar av sol- och värmestrålning och temperaturen av en svart kula i stilla luft med en molnfri himmel. Solhöjd: 10° och 30°. Symbolerna ● och ○ står för en svart modell och en modell med 50% reflektion över 20% av ytan och 20% över resten. Segmenten med 50% reflektion är riktade mot solen och är genomträngliga för solinstrålningen till 25% av pälsens tjocklek i genomsnitt. ⊙ står för samma modell men ogenomträngligt, medelvärden för slumpartig orientering. Temperaturerna är för fristående modeller (vänster) och för modeller i närheten av tätt grenverk av gran eller en, orienterad mot syd ().

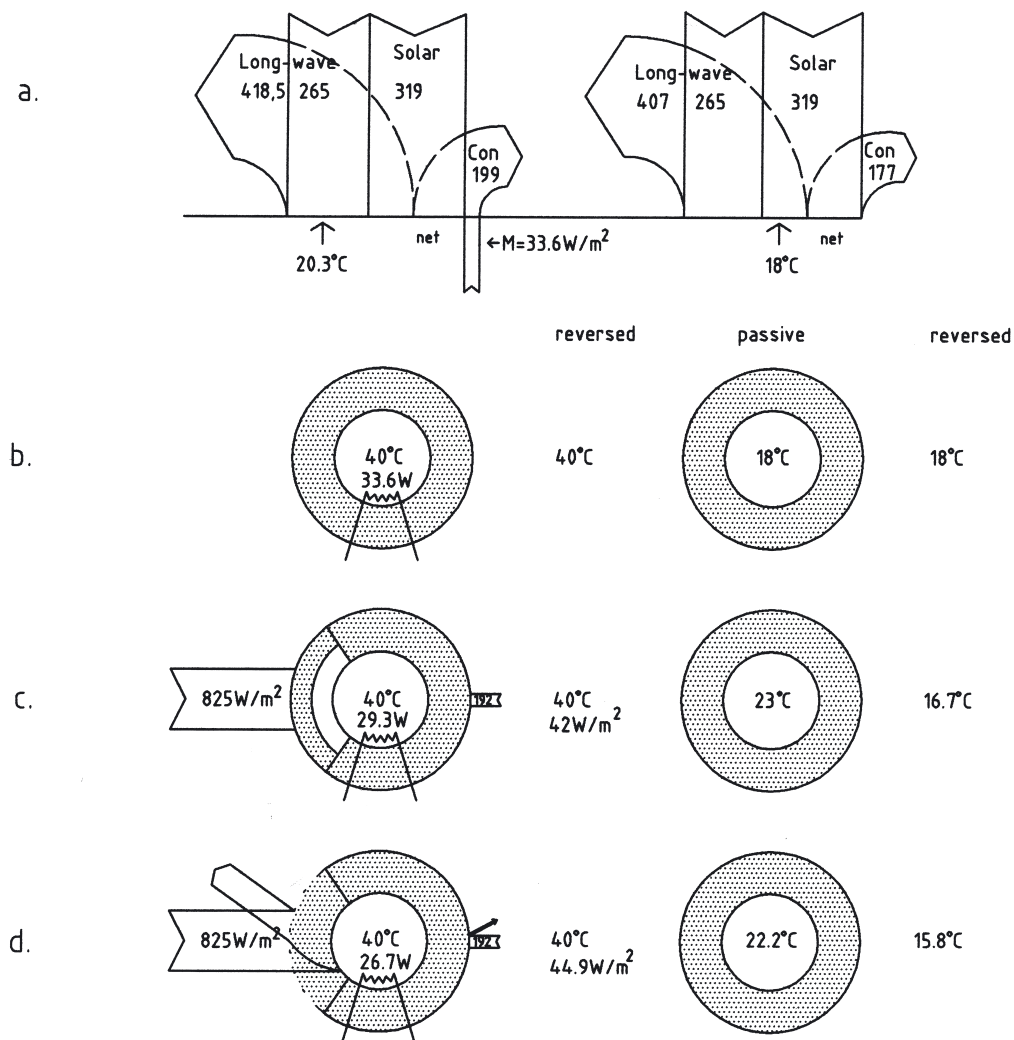


Figure 3. a. Energy fluxes [W/m²] averaged over the surface of a black standard model (see text) which is kept at a core temperature of 40 °C at an air temperature of 0 °C. The net radiation absorbed plus the heating power applied is given to the air by convection. Right side: the same for a passive (unheated) model in the same situation. The radiation conditions are the same as in Figure 2 with a solar elevation of 30°. b. The heating power needed to keep the core of the model at 40 °C together with the temperature of the unheated model. c. The same as 3b when the overall thermal conductance of a segment that constitutes 20% of the total surface is doubled. Data are shown both when this segment is facing the sun and when it is reversed. Temperatures of the unheated model are also shown. d. As 3c, but with a segment that is partially penetrable to radiation. See also legends Figure 2. The heating power is given here in W/m² of the outer surface of the Standard Model of which the surface is: 0.00896 m².

a. Energiflöden mot och från ytan av en svart standardiserad modell (se text) med en kärntemperatur av 40 °C. Flödena är medelvärden [W/m²] över den sfäriska ytan vid en lufttemperatur på 0 °C. Den absorberade nettostrålningen plus energin producerad i kärnan överförs till luften genom konvektion. Till höger: detsamma för en passiv, uppvärmd modell i samma situation. Strålningsförhållandena som i Figure 2, solhöjd 30°. b. Värmeproduktionen [W/m²] som behövs för att hålla kärnan på en konstant temperatur av 40 °C tillsammans med uppmätta temperaturer i den passiva modellen (jfr: 3a). c. Som 3a och 3b när konduktansen, C_o , i ett segment som utgör 20% av den totala ytan, är fördubblad. Värderna visas både när detta segment är riktat mot solen och vänt från denna. Solinstrålningen [W/m²] mot segmentet och resten av sfären visas separat. d. Som 3c när ett segment är delvis genomträngligt för solinstrålningen. Se också Figure 2. OBS: Värmeproduktionen beräknad i W/m² för ytan (0.00896 m²) av Standard Modellen.

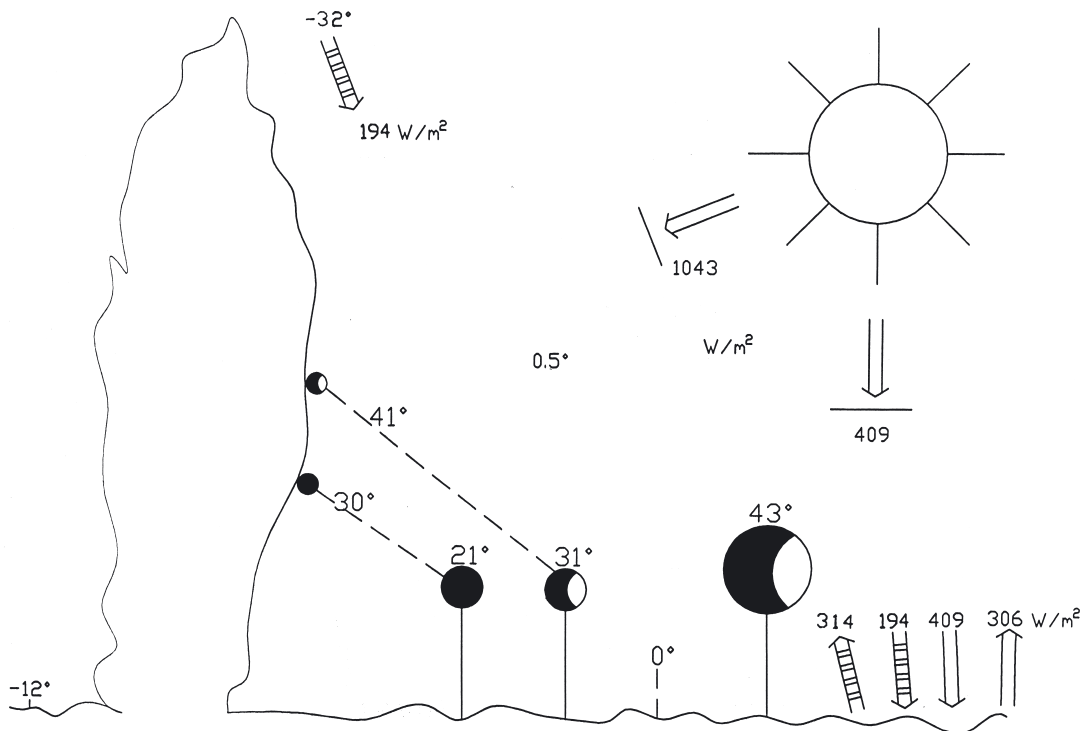


Figure 4. Radiation conditions and temperatures of black and thermally isolated bulbs on a day with closed snow cover at a solar elevation of 20°. The latter type of bulbs was partially penetrable to radiation. The upper right corner shows the solar energy received on a plane that is perpendicular to the direct rays of the sun and on horizontal planes pointing upwards (for global radiation) and downwards (for reflected radiation), respectively. The long-wave radiation emitted by the snow and received from the sky is shown by cross-hatched arrows.

Temperaturerna i svarta kulor och kulor med en isolerande skikt som var delvis genomträngliga för solinstrålningen på en sida. Mätningarna är gjorda under klar och vindstill vinterdag när marken var helt snötäckt. I övre hörnet till höger: infallande solenergi mot en yta vinkelrätt mot den direkta strålningen och mot en horisontal yta riktad uppåt (för global strålning) och nedåt (för reflekterad strålning). Den långvågiga (värme-) strålningen visas som korsstreckade pilar.

Table 1. Excess temperatures (Δt) compared to air temperature of various models in relation to those of a freely exposed black bulb.

Skillnaden (Δt) mellan lufttemperatur och temperaturen i sfäriska och delvis genomträngliga modeller, i förhållande till samma skillnad i en fritt exponerad svart kula.

Model	Δt Relative range	average	Δt Maximum °C
Black in Juniper	1.25-1.86	1.40	29.3
Fluffy grey small			
5.8 cm Ø	1.29-1.96	1.55	30.9
Fluffy white small			
5.8 cm Ø	1.34-1.87	1.54	29.3
Fluffy grey large			
12 cm Ø	1.60-2.20	1.93	43.5

Juniper (*Juniperus communis*) both the black bulb and the small fluffy model reached temperatures roughly 10 °C higher than when freely exposed. The dense (elk-browsed) surface of the Juniper had a radiative temperature of 8 °C, i.e. 40 °C higher than that of the sky. (This means that the Juniper radiates heat like a black surface of 8 °C and the thermal radiation received from above is the same as when the sky was a dome with a temperature of -32 °C).

Though the measurements were all made in southern Sweden (57° N) the situation shown in Figure 4 is probably more typical for the late winter further north. I estimate from incidental measurements that the strong effects shown in Figure 4 can be approached already with a solar elevation of 12–15 degrees when a still more stable air compensates for the lower amount of solar energy received (cf. Appendix).

Table 1 shows the excess temperatures of the fluffy models in relation to the black bulb temperature over a more extensive series of measurements. Note that the temperature excess of the white fluffy model does not differ essentially from that of the grey one. The black bulb temperature varied between 10° and 21° above air temperature, which means in non-instrumental terms: an unobscured sun, an atmosphere between very clear and somewhat turbid, and air movement indiscernible or just visible on dry grass leaves at the site of the measurements.

Discussion

As mentioned, both the axes in Figure 1 are logarithmic. For a fixed value of the quotient r_u/r_i the relation between mass, W , and overall thermal conductance, C_o , is given by a (virtually) straight line, which means that it can be expressed by the relation: $C_o = PW^s$, where P is a proportionality factor and s is the slope of the line. For $r_u/r_i = 2$ for instance, $s = 0.35$. Doubling the linear dimensions would increase the mass with a factor 8, the surface with a factor 4 and thickness of the plumage with a factor 2. That s is 0.35 and not 0.33 here is due to the fact that not only conduction but also surface related processes, heat transfer to the air and heat loss by radiation play a (minor) role here. When r_u/r_i decreases, s increases gradually as the surface related heat transfer processes become relatively more important. For an uninsulated core kept at a constant temperature s would be 0.66.

The proportionality with $W^{0.66}$ also applies approximately to the basal metabolic rate. The values given for s are here between 0.66 and 0.75 (Kendeigh

et al. 1977). The basal metabolic rate (BMR) is the lowest metabolic rate that a healthy bird can maintain regardless of the circumstances. The relation between BMR and surface would be obvious if C_o increased at the same rate, but this is definitely not the case. According to Kendeigh et al. (l.c.), $s = 0.52$ for passerines, 0.58 for non-passerines, and 0.49 for all birds, calculated from another set of data. Through my own data a line can be drawn with a slope of ~0.4. Anyway the temperature at which the BMR can fully compensate the heat loss becomes lower with increasing mass. This compensation point is called the lower critical temperature (LCT).

From Figure 1 it is clear that the overall conductance, C_o , derived from photographs is always below the trend lines derived from metabolic measurements. The difference increases with increasing mass. This could be due to the fact that smaller birds approach a spherical shape more closely than larger ones, and/or that the specific conductivity of plumage could increase with size. Another possibility is that for the larger birds the plumage was not as fully expanded in the experimental situation (at 0 °C) as it was in the field at temperatures below -5 °C and that this difference was much less for the smaller birds. Note that the metabolic measurements I refer to have been done with fasting birds. In this connection it is interesting that it is generally assumed that below the LCT the overall conductance does not increase, but, according to Dawson & Whittow (2000), 'not all birds conform to this model'. A similar remark is made by Kendeigh et al. (1977) and the common observation (e.g. Wijnandts 1984) that the relation between metabolic rate and ambient temperature is not as expected from this model can be understood by assuming that in the temperature trajectory below the LCT, there is both a decrease in overall conductance and an increase of metabolic heat production. A combination of photographic and metabolic measurements would be the best approach to test this.

For the Hawk Owl *Surnia ulula*, an r_u/r_i of 1.95 was found, quite high for a bird of this size. This is in good accordance with the low BMR and metabolic rates in general for the owls. Wijnandts (1984) found by metabolic measurements that for a Long-eared Owl *Asio otus* of 240 g, the overall conductance could be as low as 0.040 W/°C which is compatible with a thermal model with $r_u/r_i = 1.8$.

For small passerines with a body size between Goldcrest *Regulus regulus* and Great Tit, the photographic data lie only slightly below the trend line. For the species where I could retrieve specific

metabolic data from the literature (Kendeigh et al, 1977, Dawson & O'Connor, 1996), the Goldcrest, the Coal Tit *Parus ater*, the Willow Tit, the Redpoll *Carduelis flammea* and the Great Tit, the fit was practically perfect. This would mean that:

1. The specific conductivity of the plumage is estimated correctly.
2. The spherical model is close to reality.
3. The estimate of metabolic heat produced from oxygen consumption is right.
4. Heat loss via other pathways than conduction via the plumage is negligible.

The pessimistic viewpoint that all errors have compensated each other seems to be less probable, the more so as the calculated overall conductance is near the lower limit of what is possible with the given volume. Furthermore, the metabolic heat production includes the latent heat loss by evaporation, though this may be only a few percent of the total heat loss under winter conditions.

The overall conductance derived from both photographs and laboratory measurements can also be compared with measurements of the metabolic rate of free living Willow Tits and Siberian Tits *Parus cinctus* by means of the doubly labelled water method (Carlson et al. 1993; see also Dawson & O'Connor 1996). The energy produced by these birds in January near the polar circle was about 10% less than what was required to keep our thermal models warm under the same conditions. These differences could be explained by the difference between the measured air temperature at a nearby airport and the operative temperature experienced by the birds. Also, these species regularly save energy by entering a state of nocturnal hypothermia (Reinertsen and Haftorn 1986). It seems, however, most realistic to say that the results obtained by both methods support each other and also that the energy produced is used to maintain body temperature and that the energy that is lost to the environment through work performed 'outside the body' cannot be a large item on the energy balance.

The quotient r_u/r_i approaches 2.0 for the smaller birds, i.e. the linear dimensions of the naked bird are doubled by the plumage and the volume increases eightfold. Heat transfer considerations (e.g. MacAdams 1951, Monteith & Unsworth 1990) show that a further increase of the plumage thickness will not result in a corresponding lowering of the overall thermal conductance. For example a doubling of the plumage thickness (from $r_u/r_i = 2$ to $r_u/r_i = 3$) would

mean a decrease of the heat loss by of 22%. Note that the heat transported through the plumage by conduction will eventually be given off by the surface, which in the example increases by a factor $1.5^2 = 2.25$ (cf. Appendix). With increasing coat thickness the effect of better insulation is more and more counteracted by the increased outer surface, though apparently still worthwhile as the photographs of Petterson (2002) show.

The thermal model produced good quantitative results when compared to measurements on birds in a metabolic chamber. This means that it seems justified to use such models to understand the energetics of a bird in natural surroundings. To define the environmental conditions simple black bulbs, in combination with the appropriate theoretical and physical models, worked well.

Further details about the models

I start with some general remarks on the use of both the physical and the calculated thermal models that I have used in this study. For an insulated spherical model, the energy needed to keep it at a constant temperature, say 40 °C, can be readily calculated in relation to air temperature, radiation and wind (cf. Appendix). And as mentioned these factors can be combined into an effective or operative temperature (cf Figure 2). Operative temperature is used here only for real birds.

When a spherical model with a symmetrical insulating layer that is impenetrable both for wind and radiation is placed in the sun, its core temperature is equal to its effective temperature and independent of the conductance (or even the presence) of the insulating layer. This means that the temperature in the centre of an uninsulated bulb of thin metal of the same size and reflectivity will be the effective temperature.

The resemblance can be very rough if only the model absorbs as much radiation per unit surface as the bird. Thus the temperature in a blackened beer can gives a reasonable approximation of the operative temperature for a Jackdaw *Corvus monedula*, provided that the can has approximately the same size and form. When there are strong asymmetries in the properties of the plumage it is much more difficult to interpret the black bulb readings as both the orientation of the bird and the conductance of the plumage are of importance. This is demonstrated by Figure 3c where for a segment of the thermal model the overall conductance is halved. The penetrability of the plumage for solar radiation also strongly

affects the operative temperature. The absorbed radiation is more effective when the insulation on the side of the bird facing the sun is thinner or better penetrable for radiation. A more detailed analysis of these effects and relevant literature is given by Stoutjesdijk (2002). Theoretical estimates are shown in Figure 2 and 3. Measurements on physical models that are penetrable on one side (fluffy) are shown in Figure 4 and collected in Table 1. Note that the measured effects are stronger than calculated (Figure 2 and 3).

A physical model that approaches the operative temperature of a real bird can be made also in more complicated cases but such models have no longer the attractiveness of the simple black bulb. The logical step is to make an as accurate as possible imitation of the real bird. This is a copper cast of the bird's body covered by the original skin and plumage. When the core is kept at 40 °C the resemblance with the real bird is as good as possible. This 'taxidermic mount' can also be used unheated to measure the operative temperature (Bakken 1992, Wiersma & Piersma 1994).

In the following section I concentrate on smaller birds for which the agreement between the thermal properties of the real bird and the thermal model were found to be best.

In the following I refer to a 'standard model' that may be seen as representative for the rather numerous group of small passerines which survive severe winter conditions in the northern forest. The model has a r_i of 1.42 cm and a r_u of 2.67 cm ($r_u/r_i = 1.88$). Its effective temperature is with sufficient accuracy measured by a black bulb of 58 mm ϕ .

The energy needed to keep this model at 40 °C was calculated in relation to the basal metabolic rate (B.M.R.) of a bird of 12 g. Here the relation between mass (M) and B.M.R. is taken to be $B.M.R. = 0.054 M^{0.66}$ Watt after Kendeigh et al. (1977).

For the standard small 'bird' an energy production equal to the B.M.R. (0.278 W) can keep it warm (40 °C) at an air temperature of 21 °C (which then is the L.C.T.) in surroundings where solar radiation is unimportant, e.g. in dense forest. With an air temperature of about -20 °C, the required heating power will be over three times the B.M.R. which is already close to the maximum sustainable energy production (Ricklefs 1996, Drent & Daan 1980). Root (1988) concludes that many passerines are restricted to winter ranges where the long-time average of the heating power required does not exceed 2.5 B.M.R. Similar ratios are given for a wide range of birds in Dawson & O'Connor (1996),

Wiersma & Piersma (1994) and Wijnandts (1984).

The importance of solar radiation for different species

A standard model in the sun can reduce its energy loss with an amount equal to the BMR when the difference (Δt) between the effective temperature and the air temperature equals 19 °C. From the data in Figure 2, 3 and 4, it is clear that this difference is often exceeded with a clear and stable atmosphere in thermally favoured sites. For a standard model Δt can be 30 °C. A conservative estimate of the operative temperature of the smaller forest birds in the same situation would be considerably more than 20 °C above air temperature. When the fluffy model ($\Delta t = 40$ °C) in the same way represents a bird in the sun, an operative temperature of more than 30 °C above air temperature would easily be achieved. In this connection it is significant that the penetrating radiation can be quite effective even with a strongly reflective plumage (cf. Table 1) as a higher penetration depth can compensate the lower absorption. The fact that solar radiation can considerably reduce the effect of low air temperature thus seems to be sufficiently documented. On the other hand it seems quite possible that already at relatively low air temperatures it can be difficult to dissipate all the metabolic heat by conduction, especially for an active bird where it is considerably higher than B.M.R. Of course, the real bird can reduce the plumage thickness, select the best of the range of possibilities between sun and shade, or move between extremes with alternately rising or falling body temperature.

In the heart of the Scandinavian winter the possibilities to make use of the sun are often absent or of short duration. Even when the sunshine hours are not a limiting factor, the sunning behaviour can of necessity extend over only a relatively small part of a bird's working day, but the idea that short periods of relief from a constantly high energetic load may be of importance, seems worth consideration. Lawrence (1958) gives a vivid description of the sunning behaviour of Black-capped Chickadees *Parus atricapillus* in the Canadian (46° N) winter especially after very cold nights (-30 °C). 'It seemed as if the acquisition of some warmth from this external source of heat was essential before the chickadees could throw all their effort into feeding'. For an actively foraging bird the effect of sunshine may not be as high as for a sunning bird, but during longer periods the overall gain by the accumulated

effect of many brief periods of sunning may be high.

Grubb (1976) observed that windy conditions were more clearly avoided by Carolina Chickadees *Parus carolinensis* under cloudy conditions than under conditions with sunny weather. Wachob (1996) studied the Mountain Chickadee *Parus gambeli* and compared its preference for sunny sites that were either sheltered or not, and found that the sheltered sites were preferred.

The importance of solar radiation for birds in the winter is most evident where low air temperatures are combined with a clear sky and rather long days (Huertas & Diaz 2001, Carrascal et al. 2001). In Spanish mountain forests the abundance of birds in the winter was strongest in those parts of the forest where the availability of sunlit patches on the tree trunks was highest (Huertas & Diaz 2001). The relationship between abundance and solar radiation was very strong for the Short-toed Treecreeper *Certhia brachydactyla* and gradually less, in that sequence, for the Coal Tit *Parus ater*, the Crested Tit *P. cristatus*, the Nuthatch *Sitta europaea*, and the Great Spotted Woodpecker *Dendrocopos major*.

Among these species the Treecreeper is the only purely insectivorous and also the smallest one. Foraging Treecreepers had a preference for sun-exposed tree trunks when air temperatures were low but with air temperatures above 9 °C there was an increasing avoidance, i.e. they visited the sunlit patches less often than would be expected with a random choice. Carrascal et al. (2001) conclude that the birds avoid these sites because the thermal benefits are counteracted by predation risks. By sampling the arthropod fauna they could conclude that a reduced availability of prey on the sunlit sites can only to a minor degree explain a decrease in the treecreeper's preference for these sites with increasing air temperature. Remarkably, the authors do not discuss the possibility that a continuous stay in the sun may be experienced as thermal stress that the birds should avoid.

Though the predation theory is plausible enough, it is hard to imagine that the thermal conditions on, or close to, the bark of the pine trees would not significantly affect both the treecreepers and the arthropods that they eat (Stoutjesdijk 1977, Nicolai 1980). Carrascal et al. (2001) measured the temperature of dummies, clad with the plumage of a Treecreeper, and of black cylinders of the same size. Both had average excess temperatures of 14.6 °C with a standard deviation of 6 °C. This makes it quite possible that locally the operative temperature was well over 30 °C when the air temperature was 9 °C.

The fact that avoidance because of heat stress may come into play here is supported by the work of Clark (1987) who found that for Starlings *Sturnus vulgaris* there was a gradually increasing avoidance with operative temperatures over 31 °C.

In conclusion it may be said that quite elementary physical constraints may govern the life of a bird in its natural environment when it lives 'Close to the edge' (Piersma 1994). At a safe distance from this (energetic) edge many other aspects come into play.

References

- Bakken, G.S. 1976. A heat transfer analysis of animals: Unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60: 337–384.
- Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. *Amer. Zool.* 32: 194–216.
- Carlson, A., Moreno, J. & Alatalo, R.V. 1993. Winter metabolism of coniferous forest tits (Paridae) under arctic conditions: a study of doubly labeled water. *Ornis Scand.* 24: 161–164.
- Carrascal, L.M., Diaz, J.A., Huertas, D.L. & Mozetich, I. 2001. Behavioural thermoregulation by treecreepers; trade-off between saving energy and reducing crypsis. *Ecology* 82: 1642–1654.
- Clark, L. 1987. Thermal constraints on foraging in adult European starlings. *Oecologia* (Berl.) 71: 233–238.
- Dawson, W.R. & O'Connor, T.P. 1996. Energetic features of avian thermo regulatory responses. Pp 85–124 in *Avian energetics and nutritional ecology* (Carey, C., ed.). Chapman & Hall, New York.
- Dawson, W.R. & Whittow, G.C. 2000. Regulation of body temperature. Pp. 344–390 in *Sturkie's Avian Physiology fifth edition* (Whittow, G.C., ed.). Academic Press, San Diego, California.
- Drent, R.H. & Daan, S. 1980. The prudent parent. Energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- Evans, C.L. 1945. *Principles of Human Physiology*. Churchill, London.
- Fanger, P.O. 1972. *Thermal comfort*. McGraw-Hill, New York.
- Gonzales, R.R., Nishi, Y. & Gagge, A.P. 1974. Experimental evaluation of standard effective temperature. A new biometrical index of man's thermal discomfort. *Int. J. Biometeorol.* 18: 1–15.
- Evans, K.E. & Moen, A.N. 1975. Thermal exchange between Sharp-tailed Grouse (*Pedioecetes phasianellus*) and their winter environment. *Condor* 77: 160–168.
- Gavhed, D., Mäkinen, T., Holmér, J. & Rintamäki, H. 2003. Face cooling by cold wind in walking subjects. *Int. J. Biometeorol.* 47: 148–155.
- Grubb, T.C. 1976. Weather-dependent foraging behaviour of some birds wintering in a deciduous woodland: horizontal adjustments. *Condor* 78: 271–274.
- Reinertsen R.E. & Haftorn S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J Comp Physiol [B]* 156: 655–663.
- Herter, K.H. 1962. *Der Temperatursinn der Tiere*. Die neue Brehm-Bücherei. A. Ziemsen Verlag. Wittenberg. Lutherstadt.

- Hill, R.W., Beaver, D.L. & Veghte, J.H. 1980. Body surface temperatures and thermo-regulation in the Blackcapped chickadee (*Parus atricapillus*). *Physiol. Zool.* 53: 305–321.
- Huertas, D.L. & Diaz, J.A. 2001. Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. *Canadian Journal of Zoology* 79: 279–284.
- Kendeigh, S.C., Dolnik, V.R. & Gamilov, V.M. 1977. Avian energetics. Pp. 127–202 in *Granivorous birds in ecosystems* (Pinowski, J. & Kendeigh, S.C., eds.). Cambridge University Press, Cambridge.
- McAdams, W.H. 1951. *Heat transmission*. McGraw-Hill, London.
- Monteith, J.L. & Unsworth, M.H. 1990. *Principles of environmental physics*. Edward Arnold, London.
- Nicolai, W. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* (Berl.) 69: 148–160.
- Pettersson, B. 2002. Gåshuden tar fram fåglarnas dunsovsäck. *Vår Fågelvärld* 8: 30.
- Piersma, Th. 1994. *Close to the edge*. Thesis Groningen (NL) Het Open Boek, Den Burg (NL).
- Ricklefs, R.E. 1996. Avian Energetics, Ecology and Evolution. Pp. 1–24 in *Avian energetics and nutritional ecology* (Carey, C., ed.). Chapman & Hall, New York.
- Root, T. 1988. Energy constraints on avian distributions and abundance. *Ecology* 69: 330–339.
- Schmidt-Nielsen, K. 1972. *How animals work*. Cambridge University press.
- Scholander, P.F., Walters, V., Hock, R.E. & Irving, L. 1950. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* 99, 225–271.
- Snow, D.W. & Perrins, C.M. 1998. *The Birds of the Western Palearctic. Concise Edition*. Oxford University Press, Oxford.
- Stoutjesdijk, Ph. 1977. High surface temperatures in the winter and their biological significance. *Int. J. Biometeorol.* 21: 325–331.
- Stoutjesdijk, F. 2002. The ugly duckling: A thermal viewpoint. *J. Therm. Biol.* 27: 413–422.
- Stoutjesdijk, Ph. & Barkman, J.J. 1992. *Microclimate, vegetation and fauna*. Opulus Press, Knivsta, Sweden.
- Taylor, J.R.E. 1986. Thermal insulation of the down and feathers of Pygoscelid Penguin chicks and the unique properties of penguin feathers. *The Auk* 103: 160–168.
- Ulfstrand, S. 2001. Liv och död i sol och skugga. *Vår Fågelvärld* 60(8): 26–27.
- Wachob, D.G. 1996. The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *Condor* 98: 114–122.
- Walsberg, G.E., Campbell, G.S. & King, J.R. 1978. Animal Coat Color and radiative heat gain: a re-evaluation. *J. Comp. Physiol.* 126: 211–222.
- Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energi expenditure in the annual cycle of red knots. *The Condor* 96: 257–279.
- Wijnandts, H. 1984. Ecological energetics of the long-eared Owl (*Asio otus*). *Ardea* 72: 1–92.

Sammanfattning

Fåglar i kyla: Effekterna av fjäderskrudens struktur och omgivningen på den effektiva temperaturen, studerad med sfäriska modeller

När en liten fågel under en kall vinterdag burrar upp sig som en fjäderboll kan man ju fråga sig hur mycket ”levande fågel” det egentligen finns innanför? Eftersom fåglar är jämnvarma organismer kan man se dem som en kärna av levande materia som behöver hålla en konstant temperatur t.ex. 40 °C och för detta har en yttre isolering av fjädrar. En annan men närliggande fråga är då hur mycket energi detta kostar i relation till lufttemperatur, vind och strålning och vilken betydelse isoleringens (d.v.s. fjäderdräktens termiska egenskaper) då har. För en rund sfär är detta inte svårt att beräkna och frågan blir då istället i vilken utsträckning en sån modell kan representera en levande fågel från termisk synpunkt.

Jag uppskattade volymen av fri levande fåglar genom att fotografera dem i profil och sedan jämföra fotografiet med en kula av känd storlek som fotograferades med oförändrad inställning av linsen. Jag antog då att fågeln är en rund, avlång kropp, t ex oval eller äggformad. För att beräkna volymen av en sådan kropp tänker man sig att man skär den i runda skivor lodrätt genom längsaxeln. Om till exempel volymen av en talgoxe bestämdes till 90 cm³ och vikten till 18 g så antog jag att den kunde representeras av en sfärisk modell med en kärna av 18 cm³ och en inre radie, r_i , av 1,62 cm, omgiven av en isolerande mantel så att det hela formade en sfär med en yta av 90 cm³ varvid ytterradien, r_u , blev 2,78 cm. Värmeförlusten av en sån modell kan skrivas som: $C_0 (t_b - t_a)$ där t_b är temperaturen i kärnan, t_a , lufttemperaturen och strålningen har försumbar betydelse. C_0 beräknades för stillastående luft under det försiktiga antagandet att den specifika värmeledande förmågan i fjäderdräkten är den lägste som kan förekomma i tekniska eller naturliga material.

Linjerna i nomogrammet (Figur 1) visar sambandet mellan kärnvolumen i cm³ (alternativt vikt i g) och C_0 , den totala konduktansen i W per °C, för modeller med en kvot r_u/r_i mellan 1,2 och 2,0. Om vikten och det fotografiska uppskattade värdet av r_u/r_i av en fågel placeras i nomogrammet, kan värdet av C_0 avläsas. Nomogrammet visar också trendlinjer för sambandet mellan vikt och C_0 beräknade från litteraturvärden. Dessa i sin tur kommer från metaboliska mätningar i laboratorier under förhållanden (temperatur ca. 0 °C och svag luft rörelse) som gör dem jämförbara med de data jag presenterar här. Överensstämmelsen är god och avvikelserna går i den riktning som kan

förväntas. De minsta fåglarna har den relativt sett tjockaste fjäderdräkten, ofta kan en kvot r_u/r_i på 2,0 uppnås (Figur 1). En ytterligare ökning av r_u/r_i över 2,0 är föga effektiv.

Jag har använt en enkel fysisk modell för att karakterisera de termiska förhållandena för små tättingar som övervintrar i den boreala skogen. För en modell med en kärnvolum av 12 cm^3 , $r_i = 1,42 \text{ cm}$, $r_u = 2,67 \text{ cm}$, $C_0 = 0,0152 \text{ W/}^\circ\text{C}$ och en kärntemperatur t_b av $40 \text{ }^\circ\text{C}$ beräknades värmeförlusten under realistiska strålnings- och temperaturförhållanden, naturligtvis med förhoppningen att komma i närheten av förhållandena för en riktig fågel.

I en naturlig situation där strålningen och vind är av stor betydelse kan ekvationen för C_0 ovan fortfarande användas genom att byta ut lufttemperaturen (t_a) mot den sk operativa eller effektiva temperaturen (t_e) som kan ses som temperaturen som fågeln faktiskt upplever. Under förutsättning att den fysiska modellen är svart kan man använda temperaturer uppmätta i en lika stor svart kula av tunn metall som t_e i ekvationen. Sådana temperaturer bör vara mycket användbara för att karakterisera den termiska miljön för en levande fågel. Figur 2 visar bl a hur temperaturen av en svart kula ($2r_u = 5,8 \text{ cm}$) är $12 \text{ }^\circ\text{C}$ högre än lufttemperaturen när solen står 10° över horisonten. Värdet är ganska typiskt för en stilla vinterdag med en molnfri himmel och en klar atmosfär.

Under samma förhållanden men med mycket reflekterad strålning från en brant snötäckt slutning kan temperaturskillnaden, Δt , vara över $20 \text{ }^\circ\text{C}$. Om fågeln dessutom är i närheten av ett tätt grenverk kan detta ge ytterligare en temperaturhöjning. Om solen står högre på himlen kan Δt bli mycket högre. Effekten kan förstås också bli mindre om en del av solstrålningen reflekteras bort från modellens yta, men detta motverkas om det isolerande skiktet är delvis genomträngligt för solstrålning eller tunnare (Figur 3) på den sidan av fågeln som är vänd mot solen. Temperaturen i en fysisk modell kan sålunda överstiga lufttemperaturen med $40 \text{ }^\circ\text{C}$ utan värmeförlust infifrån (Figur 4).

Om t_e är ca. 20° över t_a är minskningen i energiförbrukning lika stor som basalmetabolismen hos en tätting på 12 g , och det är rimligt att anta att t_e skulle kunna vara mer än $30 \text{ }^\circ\text{C}$ över t_a för en solbadande fågel. Det är möjligt att effekten på den totala energibudgeten är liten under de korta midvinterdagarna i Skandinavien. Däremot kan den vara avsevärd under vårvintern när långa dagar kombineras med låga lufttemperaturer.

Det är också klart att redan med en lufttemperatur

av $10 \text{ }^\circ\text{C}$ kan den effektiva (upplevda) temperaturen överstiga den optimala så mycket att små fåglar måste undvika längre vistelser i solen.

Appendix

The energy fluxes to and from the outer surface of an insulated spherical model (outer radius r_u) of which the core (radius r_i) is kept at a constant temperature t_b , are shown in Figure 3. In a state of equilibrium with the environment, the heat flow from the core to the outer surface, with temperature t_s , can be written as:

$$M = a_{con}(t_b - t_s) \quad (A1)$$

where a_{con} is the conductance [W/m^2]. For an insulated sphere we have:

$$a_{con} = \frac{r_i k}{r_u(r_u - r_i)} \quad (A2)$$

where k is the specific conductivity [W/m] of the insulating material. At the surface the heat (H , W/m^2) given to the air by convection, can be expressed as:

$$H = a(t_s - t_a) \quad (A3)$$

where a [$\text{W/m}^2 \text{ }^\circ\text{C}$] is the coefficient of convective heat transfer, a decreases with size and increases with air movement (cf. Stoutjesdijk & Barkman 1992). The surface receives radiant (short-wave) energy from the sun, it emits long-wave (heat) radiation and receives long-wave radiation from the sky and the surroundings. The sum of the incoming and outgoing radiation fluxes is called the net radiation: R_{net} [W/m^2].

At the surface the sum of M and R_{net} is given to the air by convection:

$$H = \alpha(t_s - t_a) = M + R_{net} \quad (A4)$$

M can be negative i.e. directed inward. It is convenient to write:

$$R_{net} = R_{net a} - \alpha_{rad}(t_s - t_a) \quad (A5)$$

where $R_{net a}$ is the value R_{net} would have when the surface was at air temperature and α_{rad} the increase of the emitted long-wave radiation when the surface temperature increases by one $^\circ\text{C}$. For a black heated model and an unheated black bulb of the same size in the same situation $R_{net a}$ is equal. With help of the equations A1 to A5 the heat loss from the core (M , in W/m^2) can be expressed in its dependence upon the environmental parameters:

$$M = \frac{\alpha_{con}}{\alpha_{con} + \alpha + \alpha_{rad}} \{ (\alpha + \alpha_{rad})(t_b - t_a) - R_{net a} \} \quad (A6)$$

Equation (A6) can be understood to describe the local situation or the average over the surface of a sphere, as is done in Figures 3a and b. For an unheated black bulb $M=0$ when taken as an average over the sphere and the average t_s is equal to t_e , the temperature in the centre of the bulb. Furthermore:

$$t_e = t_a + R_{\text{net}} / \alpha \quad \text{or} \quad t_e = t_a + R_{\text{net}a} / (\alpha + \alpha_{\text{rad}}) \quad (\text{A7})$$

and equation A6 can be written as:

$$M = \frac{\alpha_{\text{con}}(\alpha + \alpha_{\text{rad}})(t_b - t_e)}{\alpha_{\text{con}} + \alpha + \alpha_{\text{rad}}} \quad (\text{A8})$$

Thus the temperature of a black bulb of the same size and in the same position as the heated model represents its effective temperature and it can be used to estimate t_e for a bird when allowances are made for size, reflectivity, etc. In the right hand side of equation A8, the expression:

$$\frac{\alpha_{\text{con}}(\alpha + \alpha_{\text{rad}})}{\alpha_{\text{con}} + \alpha + \alpha_{\text{rad}}} \quad (\text{A9})$$

is called C_{os} [$\text{W}/\text{m}^2 \text{ } ^\circ\text{C}$] hereafter. The overall thermal conductance as commonly used, for the whole bird, can be written in the present notation as: $C_o = S \cdot C_{\text{os}}$ [$\text{W}/^\circ\text{C}$] where S is the surface in m^2 .

From equations A2, A6, A8 and A9 it can be understood that though C_{os} can be strongly reduced, via α_{con} , by increasing the insulation thickness ($r_u - r_i$), this affects C_o much less, because S is proportional to r_u^2 , especially when α_{con} is small compared with ($\alpha + \alpha_{\text{rad}}$) and $r_u/r_i > 2$.

C_{os} is not very sensitive for wind velocity via α since α occurs both in the numerator and the denominator and α_{con} usually is rather small in comparison with α and α_{rad} . Thus, with $t_e = t_a$ and as long as the wind does not penetrate into the plumage, which increases α_{con} , there is only a weak effect on M . When, however, t_e is much higher than t_a , that is with strong sunshine, the wind effect (via α) is much stronger (cf. equation A7). A penetration of the plumage seems to occur only when the wind velocity exceeds several m/sec (cf. Bakken 1990, Wolf & Wealsberg 1996).

The simplification of averaging the fluxes over the surface of the model is only permissible when the model is fully symmetrical. When the insulating properties of the coat are not evenly distributed over

the sphere its orientation to the sun is important. Intuitively, and with the help of equations A6 and A8, it can be understood that when the heat enters easily (high α_{con}) on the sunny side and has difficult (low α_{con}) to leave on the shadowside the effect of solar radiation will be strongest (see Figure 3). The same reasoning applies when the solar radiation is more effective on one side because it penetrates the plumage (Stoutjesdijk 2002). The general relations are illustrated by some numerical data derived from measurements (Figure 3).

The conductance α_{con} is $1.7 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$, calculated from (eq. A2) with $r_u = 2.67 \text{ cm}$, $r_i = 1.42$ and $k = 0.04 \text{ W}/\text{m}$. After Gavhed et al. (2003), α_{con} of the 'Finnish winter military ensemble' is $2.4 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$. The average short-wave radiation absorbed is $319 \text{ W}/\text{m}^2$. The long-wave radiation absorbed is $265 \text{ W}/\text{m}^2$ and the emitted long-wave radiation at the black bulb temperature ($18 \text{ } ^\circ\text{C}$) is $407 \text{ W}/\text{m}^2$. The emitted long-wave radiation at an air temperature of $0 \text{ } ^\circ\text{C}$ would be $315 \text{ W}/\text{m}^2$ i.e. $92 \text{ W}/\text{m}^2$ less. Consequently R_{net} is $177 \text{ W}/\text{m}^2$ and $R_{\text{net}a}$ would be $269 \text{ W}/\text{m}^2$, $\alpha_{\text{rad}} = 92/18 = 5.1 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ and from equation A7 we get an α of $9.8 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$. From these data M (eq. A8, Figure 3a) and C_o (eq. A9) can be calculated.

With a very stable atmosphere typically when the surface of the snow is colder than the air above it and the elevation of the sun low ($10\text{--}15^\circ$), α can be as low as $8.0 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$. As furthermore α_{rad} decreases with temperature the relatively strongest effects on t_e can be expected on clear cold winter mornings (eq. A7).

In Figure 3c a spherical model which over 20% of the surface had a doubled value of C_{os} ($3.0 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$) is placed with this segment directed to the sun. The total received short-wave radiation is split up in the part received by the high-conductance segment ($825 \text{ W}/\text{m}^2$) and the rest of the sphere ($192 \text{ W}/\text{m}^2$). The average over the whole sphere is still equal to $319 \text{ W}/\text{m}^2$.

In Figure 3d the segment directed to the sun has the same C_{os} ($1.5 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$) as the rest but the solar radiation penetrates the plumage to an average of 25% of its depth. In Figure 3c and Figure 3d M is calculated separately for the two parts of the sphere and thus the heating power needed to keep it at a constant temperature or the equilibrium temperature reached by the passive model.

Habitat quality, breeding success and density in Tawny Owl *Strix aluco*

MARTIN PERSSON

Abstract

Habitat categories and songbird availability as a predictor of forest productivity were compared between Tawny Owl territories and areas not occupied by Tawny Owls near Gothenburg, south-western Sweden. There was no significant difference with regard to habitat categories. There was a significant positive correlation between density of territories and proportion of forest cover for each territory. With regard to songbird availability,

there was a significant difference between occupied and not occupied sites. Tawny Owl population density and chick production was positively correlated with songbird availability. Prey remnants from nest boxes were investigated to find out the importance of birds in the diet.

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Introduction

The Tawny Owl *Strix aluco* is a residential diet generalist that depends on trees for nesting, roosting and hunting. As territory size and thus population density in Tawny Owls are believed to be regulated in accordance with the minimum food abundance in the worst thinkable year, the density and productivity of Tawny Owl pairs may serve as an indicator of an area's richness in terms of long term food supply. The density of Tawny Owls differs across habitats from 3–6 territories per km² in closed deciduous forest to 1–2 territories in coniferous forest (e.g. Mikkola 1983, Southern 1970, Redpath 1995). As a pause-travel predator, dependent on suitable perches for hunting, Tawny Owls are furthermore highly dependent on tree cover to be able to hunt successfully. Home range sizes and reproductive success has thus previously been found to correlate strongly with fragmentation of tree vegetation. For instance, home range size of Tawny Owls in England increased from 20–30 ha in continuous woods to more than 200 ha in open farmland (Redpath 1995).

Tawny Owls mainly feed on small rodents (e.g. Southern 1954). Redpath (1995) found a negative relationship between density of small rodents and forest size. In June, when ground cover makes it hard

to catch small rodents, the proportion of birds as prey increases (Nilsson 1984).

In this study, I relate the distribution of Tawny Owl territories and their breeding success near Gothenburg, southwestern Sweden, to habitat features and songbird abundance. To investigate the importance of birds as part of diet in the studied area, prey remnants from nest boxes were analysed.

Field work and methods

Study area

The field work was carried out in Delsjöområdet close to Gothenburg in southwestern Sweden (5742N124E). Within 1900 ha, coniferous and deciduous forests are dominating around four lakes (Figure 1). Humans use parts of the area for recreation activities. Agriculture and forestry influence only a small part in the south. In the area for this study nest boxes were erected with a uniform distribution 300–1000 meters apart. Except from nest boxes, Tawny Owls accept a wide range of alternative nest sites (König et al. 1999). Therefore it can be assumed that availability of nest sites was the same for all Tawny Owls in the studied population.

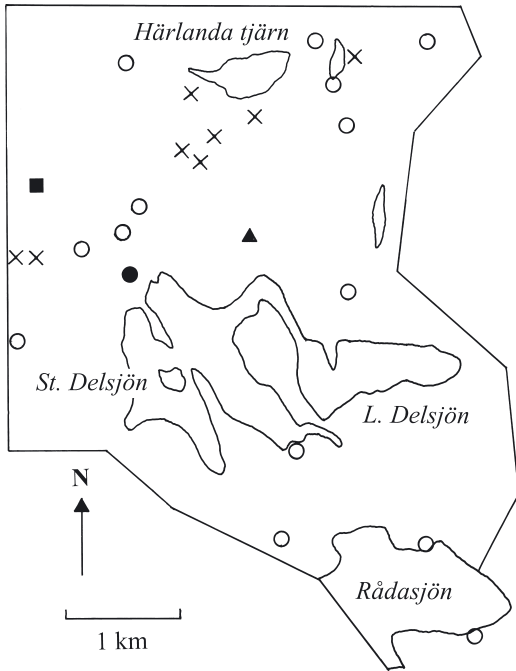


Figure 1. Map of the study area and the distribution of Tawny Owl territories in 1998–2003. Key to symbols: x = single hooting male or non-breeding pair, O = breeding in one year, ● = breeding in two years, ▲ = breeding in three years, ■ = breeding in four years.

Karta över undersökningsområdet och utbredningen av kattugglereviren 1998–2003. Symbolnyckel: x = ensam hoande hane eller icke häckande par; O = häckning under ett år; ● = häckning under två år; ▲ = häckning under tre år; ■ = häckning under fyra år.

Territory density

Occupied territories were counted using playback recordings (Redpath 1994). The area was covered with points 250–500 meters apart depending on assumptions for listening with regard to habitat and weather conditions. From each location, playback sessions of a strange male's hoot call lasted for 8 minutes. Censuses in this study were performed during clear, calm nights with optimal conditions for listening. This reduced the risk that present Tawny Owls were overlooked. The playback censuses were performed from February to March 2000 and 2001. In this study the earliest date for egg to be laid was mid February (personal observation in 2003). Thus a single hooting owl in February was taken as a

minimum criterion for an established territory. All positions of hooting males, females and breeding pairs from 1998–2003 were located using a 1:10000 map. A density index for each Tawny Owl territory was calculated from the actual territory and its four closest neighbours. For measuring the area size, a polygon encircling the five territories was drawn. Number of territories divided by the polygon area gave an index for each territory (territories/km²).

Habitat variables measured

The plant communities were investigated an area of 30 ha in each of 18 Tawny Owl territories, with the nest site in the centre, and in 10 areas of the same size where no breeding or territory-holding Tawny Owls were found. The areas not occupied were randomly selected from positions of nest boxes where no breeding was detected and no owls responded to the playback sessions. The plant community descriptions were obtained from *Park och naturförvaltningen Göteborgs kommun*. Plant communities were divided into habitat categories.

For the availability of songbirds, point counts were used (Svensson 1997). Within 18 occupied and 17 not occupied areas selected as mentioned above, all birds identified during five minutes were counted from one point in each area. The count was done twice between the end of April and mid May 2002 and once in mid April 2003. The counts began within the first hour of daylight, the time when the activity among songbirds is high, and lasted until 3 p.m. To reduce the effect of declining song activity during the day and to make the counts at different points more comparable, the counts in May were done in the opposite direction. In May the arrival of migratory birds also influenced the number. Since songbird populations does not vary much in numbers between years, the maximum number of birds counted at each site probably best shows the actual number of songbirds in the respective area. Therefore the maximum number was used as an index for the availability of birds.

Analyses of prey remnants

From 6 territories prey remnants from nest boxes were analysed. This study focuses on prey taken during the time when Tawny Owls feed chicks in the nest. In the study area, hatching varies from the second half of March (personal observation in 2003) until mid May (Persson 2000). The chicks stay in the nest for about 30 days (e.g. Southern 1970). Thus the

examined prey remnants belong to prey species taken by the owls from end of March until middle of June 1999–2003.

Prey species were identified from bones in the regurgitated pellets. For small mammals, skulls and mandibles were used, for birds bills, sternum and humerus, and for frogs the ilia. The maximum number was used as an estimate of the number of individuals eaten (e. g. Lundberg 1976).

Statistics

Tests for a difference between two groups, (i) areas occupied and (ii) areas not occupied by Tawny Owls, were made for (a) availability of songbirds and (b) proportion of landscape categories using the non-parametric Mann-Whitney *U*-test for two groups (U).

The following correlations were calculated using the non-parametric Spearman rank correlation coefficient (r_s): (a) Proportion of wooded area for each territory and Tawny Owl density, (b) Songbird availability and Tawny Owl density, and (c) Songbird availability and chick production in Tawny Owl territories.

All tests are two-tailed.

Results

Owl density and breeding success

Twenty-six Tawny Owl territories were found during the years of study. In 18 of them breeding was carried out for at least one year. The definition of breeding in this study is that at least one egg had been laid. In eight of the territories, single hooting males or pairs were noticed without any breeding. For details about the distribution of territories see Figure 1. The density of Tawny Owl varied from 0.5 to 5 territories/km². Breeding data were collected from 18 territories in the study area. The production of eggs and young for each territory are given in Table 1.

Habitat and Tawny Owl density

From the analyses of plant communities in the study area, eight habitat categories were separated: *deciduous dominated forest*, *coniferous dominated forest*, *wooded swamp*, *open swamp*, *lake-shore*, *agricultural area*, *lawn* and *built-up area*. The distribution among them is shown in Table 2. A *U*-test between areas occupied and not occupied by Tawny Owls gave no significance for a difference

Table 1. Total production of eggs and young for each territory in the study 1998–2003.

Total produktion av ägg och ungar för varje revir i studien 1998–2003.

Territory <i>Revir</i>	Eggs <i>Ägg</i>	Young <i>Ungar</i>
1	?	6
2	1	0
3	?	1
5	8	4
6	3	0
8	4	0
10	13	7
11	4	2
13	2	2
20	3	0
21	4	4
24	3	0
27	?	3
29	?	3
32	3	0
34	2	0
38	4	4
39	5	3

with regard to proportion of habitat categories. There was a significant positive correlation between density of Tawny Owl territories and proportion of forest cover for each territory (Figure 2).

Songbird abundance, Tawny Owl density and breeding success

Areas occupied by Tawny Owls generally contained a higher number of songbirds than areas not occupied areas (Table 3). The abundance of songbirds in each territory was positively correlated with both the density of Tawny Owl territories (Figure 3) and the number of chicks produced during the study (Figure 4).

Analyses of prey remnants

The total material of identified prey is given in Table 4. From the years 1999 and 2000, the material originates from one nest box each year. From 2001 data were collected from four nest boxes, and in 2003 from two. With regard to biomass, Wood Mouse *Apodemus flavicollis* and *sylvaticus* dominated as a

Table 2. The proportion (%) of habitat categories for each territory and each investigated area not occupied by Tawny Owls.

Andel (%) av habitatkategorier för varje kattugglerevir och varje undersökt område utan kattugglerevir.

With territory <i>Med revir</i>	Deciduous dominated <i>Lövskogsdominerat</i>	Coniferous dominated <i>Barrskogsdominerat</i>	Wooded swamp <i>Skogbevuxen våtmark</i>	Open swamp <i>Öppen våtmark</i>	Agricultural meadow <i>Jordbrukslandskap</i>	Lawn <i>Gräsmatta</i>	Built-up area <i>Bostadsområde</i>	Lake <i>Sjö</i>
1	45	15	5			15	20	
2	45	30					25	
3	50	40	5			5		
5	60	25			10		5	
6b	40	20	2		3	35		
8	55	20			5		20	
10	10	75	15					
11a	50	20	5			5	20	
13	25	30	5		5	15	20	
20	40		25		35			
21	20	20	20		40			
24	15	15	35	20	25			
27		30	20	50				
29	50	20	10			5		15
32	10	60	30					
34	5	75	20					
38	50	40	10					
39	30	45	20					5
Without territory <i>Utan revir</i>								
4	25	25	3		2	15	30	
6a	25	20	15		5	30	5	
7a	40	40	10		5		5	
7b	50	20			10	5	5	10
9	20	50	5					25
11b	50	25	15			5	5	
12	55	5				15	25	
16	35	20	20				5	20
23	60	40						
35		55	15					30

Table 3. Difference in songbird availability (number per point) between Tawny Owl territories and investigated areas not occupied by owls.

Skillnad i förekomst av sångfåglar (antal per punkt) mellan kattugglerevir och områden som saknade kattugglor.

	With territories <i>Med revir</i>	Without territories <i>Utan revir</i>	Significance
Mean +s.e.	12.83 ±0.71	10.3 ±0.75	U=74.5
N	18	17	p=0.05

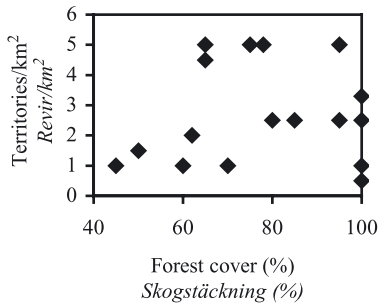


Figure 2. Correlation between Tawny Owl density and proportion of forest cover for each territory ($n=17$, $r_s=0.45$, $p<0.05$). Förhållandet mellan kattuggletäthet och andel skog i varje revir.

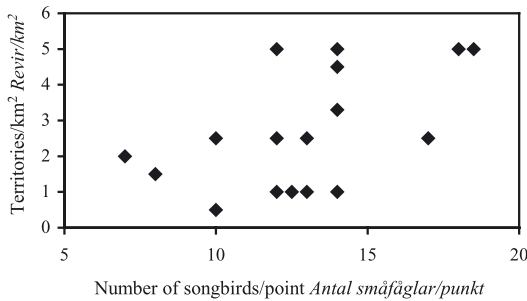


Figure 3. Correlation between Tawny Owl density and number of songbirds per point count for each territory ($n=17$, $r_s=0.56$, $p<0.02$). Förhållandet mellan kattuggletäthet och antalet sångfåglar/punkt för varje revir ($n=17$, $r_s=0.56$, $p<0.02$).

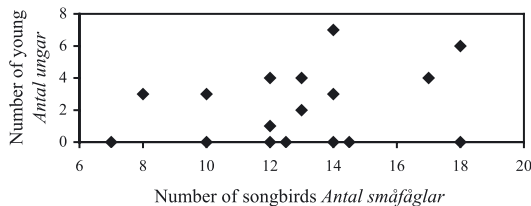


Figure 4. Total number of young produced in Tawny Owl territories during years of study correlated with number of songbirds per point count for each territory ($n=17$, $r_s=0.51$, $p<0.05$).

Totala antalet ungar producerade i kattugglerevir under åren för den här studien i förhållande till antalet sångfåglar per punkträkning i varje revir ($n=17$, $r_s=0.51$, $p<0.05$).

prey species in the study area, but birds, Field Vole *Microtus agrestis* and Bank Vole

Chletrionomys glareolus also made up a substantial part of the diet (Table 4).

Discussion

I found no significant difference between areas occupied and not occupied with regard to habitat categories defined as plant communities. Plant communities in itself may not influence breeding success or density of Tawny Owl. Tawny Owl depends on trees for roosting, nesting and hunting. All owls in this study bred in nest boxes. Availability of trees for roosting and hunting may not depend on forest type or plant species. Availability of prey, which has not been measured in this study, probably is the most important variable influencing breeding success and density in the Tawny Owl. Since the Tawny Owl is a generalist predator with a wide range of prey species (e.g. Southern 1954), most plant communities would contain food for Tawny Owls. Earlier studies have, like this study, shown a positive correlation between proportion of forest cover and Tawny Owl breeding density (e.g. Sanchez-Zapata & Calvo 1999, Repath 1995). Redpath's (1995) negative correlation between forest size and number of small rodents indicates that availability of prey is not the explanation for the relation between owl density and proportion of forest cover. If the proportion of forest increases it can be assumed that the availability of trees for nesting, roosting and hunting also increases. This may be the most probable explanation for the correlation.

The positive correlation between both density and breeding success in Tawny Owl and number of songbirds and the significant difference between areas occupied and not occupied with respect to songbirds indicate that the abundance of passerine birds may be used as an indicator of suitability and productivity of Tawny Owl habitats. Birds form, after small rodents, the second most important prey for Tawny Owls during the breeding season in this study. Since birds as part of prey increase in June the number of songbirds in each territory probably positively influences the survival of fledged young. In a study of Tengmalm's Owl *Aegolius funereus*, food conditions during the post-fledging and independence periods seemed to be crucial for the survival of the young (Korpimäki & Lagerström 1988).

Probably forest productivity not only influences songbird abundance but also the availability of small rodents which is the main food for Tawny Owls (e.g.

Table 4. Prey identified from Tawny Owl nests in Delsjöområdet, Gothenbourg, during 1999– 2003. *Identifierade byten från kattugglebon i Delsjöområdet, Göteborg, åren 1999–2003.*

Species <i>Art</i>	Unit weight	Frequency		Total biomass	
	<i>Enhetsvikt</i>	No	%	g	%
	g	<i>Antal</i>			
Bank Vole <i>Chletrionomys glareolus</i> <i>Skogssork</i>	25	56	14	1400	13
Water Vole <i>Arvicola terrestris</i> <i>Vattensork</i>	100	8	2	800	7
Field Vole <i>Microtus agrestis</i> <i>Åkersork</i>	30	58	15	1740	16
Wood Mouse <i>Apodemus sylvaticus/flavicollis</i> <i>Mindre/Större skogsmus</i>	20	151	38	3020	28
House Mouse <i>Mus musculus</i> <i>Husmus</i>	20	1	0.3	20	0.2
Brown Rat <i>Rattus norvegicus</i> <i>Brunråtta</i>	150	5	1	750	7
Common Shrew <i>Sorex araneus</i> <i>Vänlig näbbmus</i>	10	25	6	250	2
Pygmy Shrew <i>Sorex minutus</i> <i>Dvärgnäbbmus</i>	5	19	5	95	1
Water shrew <i>Neomys fodiens</i> <i>Vattennäbbmus</i>	15	1	0.3	15	0.1
Unidentified vole <i>Obestämd sork</i>	25	15	4	375	3
Amphibians <i>Groddjur</i>	20	32	8	640	6
Birds a* <i>Fåglar a*</i>	15	7	2	105	1
Birds b* <i>Fåglar b*</i>	75	18	5	1350	12
Birds c* <i>Fåglar c*</i>	175	2	1	350	3
Total <i>Summa</i>		398	100	10910	100

* Birds a = size ca Redstart (15g); Birds b = size ca thrush (75g); Birds c = size ca Wood Pigeon (175 g). *Fåglar a = storlek ca rödstjärt (15 g); Fåglar b = storlek ca trast (75 g); Fåglar c = storlek ca ringduva (175 g).*

Southern 1954). Finding a correlation between the availability of songbirds and rodents would be necessary before any conclusions could be drawn of songbirds as a predictor of Tawny Owl habitat quality.

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References

Korpimäki, E. & Lagerström, M. 1988. Survival and dispersal of fledglings of Tengmalm's Owl in relation to food conditions and hatching date. *Journal of Animal Ecology* 57: 433–441.

- König, C., Weick, F. & Becking, J. H. 1999. *Owls – A Guide to the Owls of the World*. Pica press. Sussex.
- Lundberg, A. 1976. Breeding success and prey availability in a Ural Owl *Strix uralensis* Pall. Population in Central Sweden. *ZOON* 4: 65–72.
- Mikkola, H. 1983. *Owls of Europe*. Poyser. Calton.
- Nilsson, I. N. 1984. Kattugglans bytesval ur olika perspektiv. *Viltnytt* 19: 36–41.
- Persson, M. 2000. Häckande kattugglor i skogsområden runt Härlanda tjärn, Delsjöarna och Rådasjön 1998–2000. *Fåglar på västkusten* 3: 124–126.
- Redpath, S. M. 1994. Censusing Tawny Owls *Strix aluco* by the use of imitation calls. *Bird Study* 41: 192–198.
- Redpath, S. M. 1995. Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. *Journal of Animal Ecology* 64: 652–661.
- Sánchez-Zapata, J. A. & Calvo, J. F. 1999. Rocks and trees: habitat response of Tawny Owls *Strix aluco* in semiarid landscapes. *Ornis Fennica* 76: 79–87.
- Southern, H. N. 1954. Tawny owls and their prey. *Ibis* 96: 384–410.
- Southern, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool. Lond.* 162: 197–285.
- Svensson, S. 1997. Fågelinventeringar. Chapter 19 in *Fåglarnas ekologi* (Ekman, J. & Lundberg, A., editors). Vår fågelvärld, supplement 26. Stockholm.
- Wendland, V. 1984. The influence of prey fluctuations on the breeding success of the Tawny Owl, *Strix aluco*. *Ibis* 126: 284–295.

Sammanfattning

Habitatkvalitet, häckningsframgång och täthet hos kattuggla

Kattugglan *Strix aluco* är en resident bytesgeneralist, beroende av träd för boplats och jakt. Förekomsten av kattugglor varierar mellan olika habitatkategorier med högst täthet i slutet lövskog. I den här studien relateras kattugglans täthet och häcknings-

framgång till habitatval och förekomst av sångfåglar. På en yta av 1900 ha i närheten av Göteborg sattes kattuggleholkar ut på ett avstånd av 300–1000 meter från varandra.

Kattugglerevir inventerades genom uppspelning av en främmande hanes läte. Positioner för responderande ugglor samt konstaterade häckningar markerades på en karta (Figur 1). För bestämning av habitatkategorier användes en vegetationsbeskrivning över området framtagna av Park och naturförvaltningen, Göteborgs kommun.

Antalet ägg och ungar producerade i varje revir under åren för studien användes som ett mått på häckningsframgången (Tabell 1). Efter häckning analyserades bytesrester från boplatser i syfte att utvärdera vikten av fåglar i kattugglans diet.

Det var ingen signifikant skillnad mellan habitatkategorier i kattugglereviren jämfört med områden utan kattugglor. Mellan andelen skog i reviren och tätheten av kattugglor fanns en signifikant positiv korrelation (Figur 2).

Förekomsten av sångfåglar var signifikant högre i kattugglereviren jämfört med de områden där kattugglor saknades (Tabell 3). Kattugglans täthet och häckningsframgång korrelerade positivt med förekomsten av sångfåglar i reviren (Figur 3 och 4). Analysen av bytesmaterial visade att fåglar utgör knappt 20% av den totala bytesmängd under häckningssäsongen i studieområdet (Tabell 4).

Skillnaden mellan områden med respektive utan kattugglor avseende förekomst av sångfåglar och den positiva korrelationen mellan dem och kattugglans täthet och häckningsframgång ger en indikation om att tättingar kan fungera som en indikator för bra kattugglebiotoper.

