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Höstbiologi och sångaktivitet hos svart rödstjärt *Phoenicurus ochruros* i sydvästra Sverige

REINO ANDERSSON

Abstract

I studied autumn biology of Black Redstarts *Phoenicurus ochruros*, i.e. territorial behaviour, song activity, flock structure, and social interactions. In spring, I located 105 previously colour-ringed territorial males and determined their breeding success. Of them, 34 (32%) were also seen the following autumn, and 15 (44%) of them returned next spring. Of 71 males present in spring that were not observed in autumn, 20% returned the following spring. The birds present in autumn produced 5.2 fledged young per breeding pair the next spring, compared to 3.7 for birds not present. A large proportion of the surplus of autumn individuals are probably yearlings that move from the place of birth before body moult. In autumn, aggressive behaviour occurs to a low extent among adult males when in flocks (e.g. at timber stores with high insect abundance). That individuals move between such food rich sites indicates high flexibility in autumn home ranges. The main purpose of song in autumn seems to be to monopolise rich food sites, which will increase their survival chances and may improve reproductive success the following spring.

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Inledning

Svart rödstjärt är ovanlig bland svenska tättingar, då den har en utpräglad sångperiod både vår och höst. Sång förekommer under sensommar och höst hos ytterligare några arter, t.ex. gärdsmyg, gransångare, rödhake och koltrast (Snow 1958, Lack 1965, Cramp 1988). Höstsångens uppkomst och funktion har diskuterats i olika sammanhang, men företeelsen har sällan studerats i detalj. Weggler (1997) föreslår att utvecklandet av revirbeteenden under hösten inskränker sig till arter som är kvar på sina revir åtskilliga veckor efter häckningssäsongens slut. Förändringar i t.ex. dagslängd och hormonhalt är de fysiologiska mekanismer (proximata faktorer) som utlöser sångbeteende hos fåglar under hösten (Silverin 1997). Men varför sjunger då vissa fåglar på hösten (d.v.s. vilka är de ultimata faktorerna)? Att sjunga innebär kostnader för den enskilda individen, t.ex. ökad predationsrisk, något som fåglarna måste kompenseras för på annat sätt. Sången anses ge reproduktiva fördelar under kommande säsong, i synnerhet hos arter som tillbringar vintern i sitt häckningsområde (Hegner & Wingfield 1986, Logan & Hyatt 1991). Weggler (1997, 2000) framhåller att svarta rödstjärtens höstsång och revirförsvar i schweiziska Alperna medför individuella fördelar inför nästa års reproduktion (jfr. Landmann 1996, Bergmann 1999). Men även hos flyttande arter som lövsångare, anses hannars reviretablering sent på sommaren vara betydelsefull först under påföljande vår (Lawn 1982, 1994). En annan tänkbar, men kanske mindre sannolik, förklaring till svarta rödstjärtens höstsång i Sverige är att den inte har någon funktion i detta område. Kanske bibehålls ett revirbeteende som uppkommit i södra Europa, där svarta rödstjärten i viss utsträckning är stannfågel, i vårt nordliga utbredningsområde, t.ex. genom att individer födda längre söderut i Europa förlänger sin flyttning och etablerar sig i Sverige.

Fåglars biologi under hösten är förhållandevis dåligt studerad. Svarta rödstjärtens höstbiologi och generella uppträdande är intressant, då det endast berörts i ett fåtal sammanhang (Glutz von Blotzheim 1988, Landmann 1996, Weggler 2000). Detta gäller t.ex. den sociala struktur som uppstår då svarta rödstjärtar uppträder i flock under hösten. Men också konkurrens- och dominansförhållanden gentemot andra arter är aspekter som är värda att ägnas fortsatta studier.

För att klargöra höstbiologin och sångens betydelse hos en västsvensk population av svart rödstjärt studerades bl.a. sångaktivitet, flockstruktur och ursprung för tidigare kända (färgringmärkta) individer. Arten har i Västsverige varit föremål för ingående studier de senaste två decennierna. Beskrivningar av denna populations häckningsbiologi har presenterats i en rad uppsatser (Andersson 1982, 1983, 1985a,b, 1986, 1987, 1990, 1995, 1996). Detta är dock den första studien som utförligt behandlar svarta rödstjärtens höstbiologi i Sverige.

Material och metoder

Undersökningsområdet omfattar Göteborgs hamn och närbelägna fabriksmiljöer på Hisingen samt Varbergs hamn med omgivande industriområden. Under perioden 1 september–20 november åren 1983–1997 kontrollerades närvaron av svarta rödstjärtar i genomsnitt var femte dag (11 av åren) i sammanlagt 45 kända revir. Fyra år (1988, 1990, 1993, 1994) gjordes dock betydligt färre besök, vilket innebar att kontroller ägde rum i genomsnitt var tolfte dag. Reviren fördelade sig på 21 optimala och 24 suboptimala miljöer, enligt en tidigare genomförd kvalitetsklassning under häckningstid. Kvalitetsklassningen baserades på en poängskala från 1 till 30, där optimala revir hade mellan 8 och 30 poäng (Andersson 1995).

Denna studie baseras huvudsakligen på 254 registreringar av hannar som kunde iakttas i minst 30 minuter vid ett enskilt observationstillfälle. Vid varje observationstillfälle bokfördes alla iakttagelser av sångaktivitet, sällskapande individer, revirstrider, flockbildning och sociala relationer. Fördelning per undersökningsområde och år framgår av Tabell 1. Av dessa 254 registreringar utgjordes 69 av färgringmärkta fåglar (43 olika individer) och resterande 185 av omärkta individer. Det verkliga antalet hannar som ingår i materialet kunde således inte fastställas med säkerhet.

För att få en mer detaljerad bild av höstfåglarnas ursprung och deras framgång den kommande häckningssäsongen, gjordes en speciell granskning av fåglar som färgmärkts tidigare under vårsäsongen. Detta material utgjordes av 105 revirhållande adulta hannar (2K+), 20 adulta honor (2K+) och 188 årsungar (1K) ringmärkta i boet. Dessutom ingår 21 fåglar som färgmärkts under hösten i materialet. Hannarna dominerar denna studie eftersom de uppträder mer exponerat än honorna (t.ex. vid sång och revirförsvar) och är lättare att könsbestämma i fält. De relativt få honor som berörs i uppsatsen grundar sig därför uteslutande på färgmärkta individer.

Under hösten då ruggningen avslutats har alla äldre hannar (2K+) anlagt en adult, utfärgad dräkt. Majoriteten av de unga hannarna (1K) ruggar till en gråbrun, honfärgad dräkt och går därefter inte att könsbestämma. Däremot kan de identifieras som hannar med hjälp av sången eftersom honor inte sjunger (Glutz von Blotzheim 1988). En viss andel anlägger dock delvis en utfärgad handräkt (s.k. paradoxus) i sin första partiella ruggning av kroppsfjädrarna. I tyska städer uppgår andelen paradoxus till 12% (Nicolai 1996), vilket har visat sig överensstämma väl även med andelen i västra Sverige.

Med sångfrekvens avses i denna uppsats antal sångstrofer per tidsenhet, medan begreppet sångförekomst avser om sångstrofer hörts från en hanne eller inte vid ett observationstillfälle. En geografisk förflyttning av reviret anses ha ägt rum i fall där hannen flyttat sig mer än 300 meter. Benämningen flock nedan avser ansamlingar av fåglar med sociala interaktioner som uppträder i täta (några tiotal meters) eller mer löst sammanhållna grupperingar (maximalt med något hundratal meters mellanrum). Bandspelare med uppspelad sång har använts sporadiskt vid fångst samt vid vissa aggressionstester.

För statistiska test har jag använt χ^2-test (i alla dessa test har jag använt Yates korrigering) och tvåsidig Mann-Whitney U-test.

Tabell 1. Årsvis fördelning av registrerade hannar av svart rödstjärt i Göteborg och Varberg.
Annual distribution of recorded male Black Redstarts in Gothenburg and Varberg.

År *Year*	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	Totalt
Göteborg	30	17	16	15												78
Varberg					11	7	11	9	22	10	9	6	32	24	35	176
Totalt																254

Timmerupplag i Varbergs hamn. Sådana timmerupplag utgör en insektsrik miljö för svarta rödstjärten under hösten, då fåglar i glesa flockar kan söka föda nära varandra utan större aggressioner. Men hanarna sjunger också normal revirsång på hösten, vilket kan vara ett sätt att etablera födorika revir för framgångsrik häckning följande vår.
Timber store at the harbour of Varberg. Such habitats are rich in insects in the autumn, and loose assemblies of Black Redstarts may feed together without much aggression. But the males also perform normal territorial song, which may be sign of territorial establishment for successful breeding next spring.

Resultat

Allmänt uppträdande

Lugna, klara, varma höstdagar rådde ofta en sjudande aktivitet i de revir som tidigare under säsongen endast hyst ett häckande par eller en oparad hanne. Oavsett om svarta rödstjärtar uppträdde ensamma eller i sällskap med andra, uppfattades deras beteende som intensivt och iögonfallande. Då och då ljöd sångstrofer, lika fullödiga som på våren. Fåglarna höll mestadels till i marknivå, där det pågick ett ständigt sökande efter föda på upplagsplatser och andra öppna ytor. Från att ena stunden ha exponerat sig i sina upprätta hållningar med knixande stjärtdaller, kunde de plötsligt försvinna ned på marken och tycktes emellanåt vara som uppslukade bland fabrikstomternas bråte. Strax därpå dök de upp igen, lika hastigt som de försvann, och det var årsungarna med sina kortvariga jakter som i mångt och mycket präglade områdena. Vid exceptionella koncentrationer av föda, t.ex. timmerupplag med rik tillgång på insekter, samlades fåglar flockvis tillsammans med andra arter som stenskvättor, rödhakar och rödstjärtar. Särskilt stenskvättorna kunde vara talrika och sågs då ofta indragna i smärre stridigheter och dominansbeteenden gentemot de mer underlägsna svarta rödstjärtarna.

Förekomst och sångaktivitet

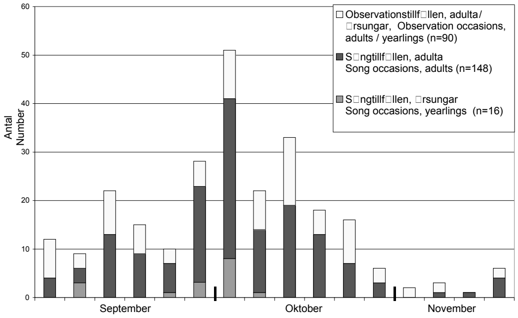
Bland de 254 höstobservationerna av hannar ingick 16 hontecknade årsungar och 16 med paradoxusdräkt. En viss andel hontecknade hannar har dock med all säkerhet förbisetts (se Material och metoder). Sång konstaterades vid 165 tillfällen (65%). I 16 fall var det årsungar som sjöng, vilket motsvarar 10% av samtliga sångtillfällen. Av Figur 1 framgår att såväl observationer av hannar som registreringar av aktiv sång kulminerade i slutet av september och början av oktober. Under två av de femton åren förekom sång ända in i november, då endast av adulta hannar.

Årsungarnas sångaktivitet fördelade sig något annorlunda jämfört med äldre hannar då de upphörde med att sjunga redan i början av oktober, trots att enstaka individer observerades in i november. Hos årsungarna var både sångfrekvens och sångförekomst oftast lägre och stroferna mer trevande jämfört med de äldre hannarna. I något fall framfördes dock intensiv sång rik på härmningar även från årsungar. Svart rödstjärt härmar sällan andra arter, men imitationer hördes några gånger hos äldre och yngre hannar under de aktuella höstarna.

Jag noterade skillnader i sångförekomst beroende på om fåglarna uppträdde ensamma eller i flock. Årsungar hördes oftare sjunga när de var i flock, medan adulta hannar uppvisade en högre sångförekomst när de var ensamma i sina revir (årsungar: $\chi^2_{(1)}=7{,}47$, p=0,063, n=23; adulta: $\chi^2_{(1)}=4{,}51$, p=0,034, n=37; Tabell 2). Sju av de 10 adulta hannar som skiftade revir mellan vår och höst konstaterades sjunga (se nedan).

Revirkvalitet

Majoriteten (83%) av alla hannar som höll revir på hösten återfanns i optimala revir, och resterande i suboptimala revir. Enbart observerade årsungar hade i medeltal 13,1 revirpoäng, sjungande årsungar 15,3, observerade adulta hannar 19,5 och sjungande adulta hannar 22,7. Av årsungarna uppehöll sig 69% i optimala revir med en genomsnittlig revirpoäng på 14,2, medan 86% av de adulta hannarna befann sig i optimala revir med en genomsnittlig revirpoäng på 21,1 (Mann-Whitney U-test, p=0,015, n=23 årsungar och 37 adulta).



Figur 1. Svart rödstjärthannars förekomst och sångaktivitet under hösten, fördelat på femdagarsperioder.
Occurrence and song activity in male Black Redstarts during the autumn (five-day periods).

Flockstruktur och revirstrider

Vid drygt hälften av de 254 observationstillfällena uppträdde hannarna i flockar av varierande storlek. Flockstorleken var oftast 2–5 fåglar, medan de största flockarna innehöll upp till 25 individer (Tabell 2). Den genomsnittliga flockstorleken uppgick till 5,6 individer.

De 44 fåglar som sågs i flockar med >5 ex, återfanns påfallande ofta i födorika revir jämfört med ensamma individer eller mindre grupper. Av dessa fåglar uppehöll sig 26 vid insektsrika timmerupplag och 15 på varv med balk- och skrotupplag där marken var mossbevuxen och bl.a. hyste stora mängder spindlar (jämför Nicolai 1992b). Även utsprängda bergsbranter med sparsam vegetation i anslutning till varvsupplag föreföll rika på insekter och var uppenbart attraktiva för födosök.

Flockarnas sammansättning framgår av Figur 2. Cirka 80% av alla fåglar utgjordes av hontecknade individer, varav en avsevärd andel sannolikt är årsungar av bägge könen. När det gäller sociala relationer inom flockarna uppträdde tidigare grannhannar vid ett tiotal tillfällen tillsammans i grupper med andra individer. Häckande par uppträdde ibland sida vid sida med någon av sina egna ungar. Och även syskon visade sig vid ett par tillfällen hålla ihop i en och samma flock – i ett fall uppträdde två syskonpar tillsammans.

Vid större ansamlingar iakttogs aldrig några egentliga revirstrider. Sådana var över huvud taget sällsynta under hösten och konstaterades endast i 3% av de 254 observationstillfällena. Stridigheterna utspelades uteslutande mellan grannhannar i högkvalitativa revir. Fem av de inblandade var 3K+ och tre 2K, fem hade tidigare häckat medan tre varit oparade.

Höstfåglarnas ursprung

Av 105 revirhävdande och individmärkta hannar under vårsäsongen observerades 34 (32%) under hösten (Tabell 3). De övriga individerna försvann från sina revir under sommaren och mediandatum för när de försvann var 26 juni.

Höstnärvaron kunde kopplas till häckningsstatusen under våren samma år hos 2K men inte hos 3K+

Tabell 2. Svart rödstjärthannars sångbeteende när de uppträder solitärt respektive i flock.
Song behaviour in male Black Redstarts when appearing solitary or in groups.

	Flockstorlek *Group size*						
Antal ind. *No. of inds.*	1	2–5	6–10	11–15	16–20	21–25	Totalt
Årsungar *Yearlings*							
Sjungande *Singing*	2	7	7				16
Bara sedda *Only seen*	13	2	1				16
Adulta *Adults*							
Sjungande *Singing*	102	30	15	1		1	149
Bara sedda *Only seen*	20	34	11	8			73
Totalt	137	73	34	9		1	254

hannar. Bland tidigare oparade 2K hannar observerades 15% under hösten, medan 52% av de tidigare häckande 2K hannarna observerades under hösten ($\chi^2_{(1)}$=8,93, p=0,028, n=55). Bland 3K+ hannar var det dock ingen skillnad i observationsfrekvens under hösten mellan hannar som häckat respektive varit oparade under våren ($\chi^2_{(1)}$=0,33, p=0,56, n=50). Majoriteten av hösthannarna (74%), utgjordes av individer som under våren häckat i högkvalitativa revir. Tiden som hannarna stannade i höstreviren varierade mellan 1 och 70 dygn (medel 11,4 dygn). Drygt hälften av hannarna observerades dock endast några få dygn (Tabell 4).

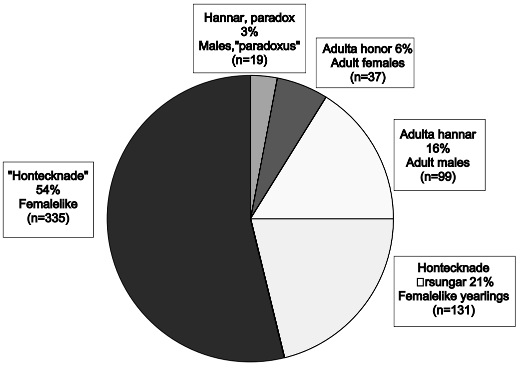
Nitton av totalt 188 (10%) färgmärkta boungar påträffades under hösten. De uppehöll sig i genomsnitt 6,0 dygn på samma plats, vilket är hälften så lång tid som de adulta hannarna (Mann-Whitney U-test, p=0,012, n=19 årsungar och 34 adulta). Sjutton av årsungarna iakttogs dock endast 1 dygn, medan de återstående två årsungarna stannade kvar 29 respektive 68 dygn. Vidare observerades under hösten 40% av de 20 honor som häckade tidigare under våren (n=14 2K och 6 3K+). Honorna stannade i genomsnitt 14.8 dygn under hösten, med en variation mellan 1 och 54 dygn (Tabell 3 och 4).

Förflyttningar mellan vår och höst

Geografiska förflyttningar mellan vår och höst förekom hos hälften av de 61 närvarande höstfåglarna med känt ursprung (Tabell 5). En del av dem hade då uppsökt särskilt födorika platser (jämför Flockstruktur och revirstrider). Tio av de 34 hannarna (29%) hade rört sig till en ny plats, men de flesta var kvar i sina vårrevir. Bland dem som skiftade fanns såväl 2K som 3K+, liksom oparade och häckande fåglar. Avståndet för förflyttningarna varierade mellan 300 och 2000 meter med ett genomsnitt på 780 meter. Hos tre hannar konstaterades successiva förflyttningar mellan flera olika revir inom ett område samma höst, troligen beroende på var födokoncentrationerna för tillfället var som störst.

Sjutton av 19 årsungar (89%) hade rört sig från födelseplatsen till en ny höstlokal. Avståndet varierade mellan 300 och 7000 meter, med ett medeltal på 1280 meter för förstakullar och 360 meter för andrakullar. Fyra av dem uppehöll sig på flera olika lokaler under hösten.

Bland de åtta adulta honorna hade tre förflyttat sig 300–700 meter (medel 530 meter), medan de resterande fem var kvar i sina tidigare häckrevir (Tabell 5).



Figur 2. Svart rödstjärtflockars uppdelning i olika köns- och ålderskategorier.
Black Redstart groups divided into sex and age categories.

Tabell 3. Färgringmärkta svarta rödstjärtars närvaro i studieområdet mellan vår och höst säsonger.
Presence of colour-ringed Black Redstarts in the study area between spring and autumn seasons.

	Vår *Spring*	Höst *Autumn*	Påföljande vår *Following spring*
Hannar *Males*			
2K oparad *2y unpaired*	34	5	8
3K+ oparad *3y or older, unpaired*	15	4	2
2K häckande *2y breeding*	21	11	7
3K+ häckande *3y or older breeding*	35	14	12
Totalt hannar *Total males*	105	34	29
Årsungar *Yearlings*	188	19	1
Honor *Females*	20	8	2
Totalt	313	61	32

Återkomst och häckningsframgång påföljande vår

Femton av de 34 hannar som stannade under hösten (44%) återkom till undersökningsområdet påföljande vår (Tabell 6). De hannar som inte bytt revir föregående säsong var tillbaka i samma revir. Sex av hannarna hade tidigare bytt revir mellan vår och höst. I ett fall återvände hannen till sitt höstrevir, medan resterande fem återvände till föregående års vårrevir. Fjorton (20%) av de 71 hannar som försvann under häckningssäsongen återvände nästa vår, vilket är en signifikant lägre andel än för de kända hösthannarna ($\chi^2_{(1)}$=5,68, p=0,0172, n=105). Hälften av dem hade då bytt revir jämfört med fjolåret.

Bland de 29 hannarna som återkom följande vår var ankomstdatum och andelen häckande likartad mellan de som hade stannat kvar under hösten respektive lämnat området föregående sommar. Höstfåglarna producerade i genomsnitt 5,2 flygga ungar per häckande par påföljande vår, jämfört med 3,7 flygga ungar per häckande par för de hannar som lämnat området föregående sommar. Denna skillnad var dock ej signifikant (Mann-Whitney U-test, p=0,28, n=10 och 9; Tabell 6).

En av de 19 höstnärvarande årsungarna återupptäcktes följande vår i ett revir som var beläget endast 600 meter från höstlokalen, vilken också var dess födelseplats. Där lyckades den få fram en rekordstor kull på sex flygga ungar. Två av de åtta honorna, som båda hade bytt till en ny höstlokal, återvände till sina vårrevir, medan resterande honor försvann.

Tabell 4. Färgringmärkta svarta rödstjärtars tidsmässiga närvaro under hösten.
Presence of colour-ringed Black Redstarts in autumn.

Antal dagar *No days*	1	–5	–10	–15	–20	–25	–30	–40	–50	–60	–70	Totalt
Hannar *Males*												
2K oparad *2y unpaired*	3			2			1					6
3K+ oparad *3y or older unpaired*	2		1									3
2K häckande *2y breeding*	6	1	3								1	11
3K+ häckande *3y or older breeding*	6	1	2	1		1		1	1	1		14
Totalt hannar *Total males*	17	2	6	3		1	1	1	1	1	1	34
Årsungar *Yearlings*	17						1				1	19
Honor *Females*	5						2			1		8
Totalt	39	2	6	3		1	4	1	1	2	2	61

Tabell 5. Färgringmärkta svarta rödstjärtars geografiska förflyttningar mellan vår och höst.
Distances of movements in colour-ringed Black Redstarts between spring and autumn.

Meter *Meters*	0–300	–400	–600	–800	–1000	–1500	–2000	>2000	Totalt
Hannar *Males*									
2K oparade *2y unpaired*	4						1		5
3K+ oparade *3y or older unpaired*	2		1			1			4
2K häckande *2y breeding*	6	1	3		1				11
3K+ häckande *3y or older breeding*	12	2							14
Totalt hannar *Total males*	24	3	4		1	1	1		34
Årsungar *Yearlings*	2	7	6		2			2	19
Honor *Females*	5	1	1	1					8
Totalt	31	11	11	1	3	1	1	2	61

Diskussion

Svarta rödstjärtens höstsång i Västsverige inleds i början av september, kulminerar kring månadsskiftet och avtar sedan successivt fram till bortflyttningen i slutet av oktober. Ett fåtal hannar dröjer sig dock kvar vissa år och kan då sjunga in i november. Sångkulmen nås ungefär vid samma tid på säsongen över stora delar av Europa, medan däremot tidpunkten för början och avslutning av sångperioden varierar (Gnielka 1968, Nicolai 1992a, Weggler 1997). Sångfrekvensen i de schweiziska Alperna under hösten motsvarar den i maj–juni, vilket innebär en halvering av sångaktiviteten jämfört med toppen som infaller i mars–april (Weggler 2000). Majoriteten av de västsvenska hannarna återfinns i optimala revir (jfr. Andersson 1995), där adulta individer med hög sångförekomst har revir av högst status.

Höstsången hos adulta hannar framförs oftast då de uppträder solitärt i reviren. Revirstrider är dock påfallande fåtaliga och förekommer uteslutande mellan grannhannar i optimala revir. Under hösten då föda förekommer koncentrerat uppträder de svarta rödstjärtarna ofta i flockar. Äldre hannar sjunger då mera sällan än när de uppträder solitärt i sina revir. Aggressionstester med bandspelare utlöser en relativt kraftig reaktion hos hannar som uppträder ensamma i sina revir, medan flockindivider endast visar sig nyfikna en kort stund (R. Andersson, opubl.). Observationer av att revirförsvar bryter samman vid höga lokala tätheter överensstämmer väl med teorier framlagda av Brown (1964), återgivna av Krebs & Davies (1987). Hans modell förutsäger att försvar av ett område (resurs) inte bör förekomma vid alltför låg, eller hög, födotäthet, utan främst vid intermediära förekomster.

Hos årsungar är höstsång inte så vanligt förekommande, och den har mer karaktären av subsång,

Tabell 6. Häckningsframgång hos återvändande färgringmärkta svart rödstjärthannar under våren i relation till deras förekomst föregående höst.
Breeding success in colour-ringed male Black Redstarts in spring in relation to their presence or absence the preceding autumn.

	Status föregående höst *Status in previous autumn*	
	Närvarande *Present*	Saknades *Missing*
Antal föregående vår *Number previous spring*	34	71
Påföljande vår *Following spring*		
Antal återkom *Number returned*	15	14
Ankomstdatum *Arrival date*	22 April	23 April
Häckande *Breeding*	10 (67%)	9 (64%)
Oparade *Unpaired*	5 (33%)	5 (36%)
Flygga ungar per häckande par *Fledglings per breeding pair*	5,2	3,7

vilken enligt Nicolai (1992a) bör betraktas som ett led i sånginlärningen. Att deras sång upphör redan i början av oktober, överensstämmer väl med att denna process normalt brukar avslutas före de uppnått en ålder av 120 dygn (Nicolai 1992a). Cucco & Malacarne (1999) anger dock att ettåriga hannars sång skiljer sig väsentligt från äldre fåglars, vilket innebär att sången utvecklas även efter första höstens inlärningsperiod. Nicolai (1992a) menar att en återupptagen sångutveckling skulle kunna gälla för sena kullar som hamnar i tidsnöd, på samma sätt som Thielcke & Krome (1989) beskrivit hos bofinken. I Västsverige sjunger årsungarna, till skillnad från de adulta, oftare då de vistas i flock. En tolkning kan vara att de stimulerar varandra när de är tillsammans och hör andra hannar sjunga.

Flockbildningen bidrar i hög grad till förståelsen av de svarta rödstjärtarnas höstbiologi i Sverige. I dessa ansamlingar uppstår en struktur av tillfälliga sociala grupperingar med lokala fåglar, t.ex. tidigare grannhannar, tidigare häckande par och årsungar födda i området. Närvaro av kända fåglar från mer avlägsna revir inom undersökningsområdet har också kunnat beläggas, bl.a. en årsunge som uppehöll sig i en flock sju kilometer från sin födelseplats. Även äldre hannar har påträffats på sådana platser flera kilometer från sina vårrevir. Det förekommer dessutom ett stort antal främmande individer, vilka delvis kan hänföras till ett tillskott utifrån. Varifrån dessa fåglar kommer är ovisst, och deras andel i flockarna svårbedömd eftersom de inte kan följas individuellt. Det är emellertid inte helt givet att dessa individer utgörs av genomflyttande fåglar norrifrån. Åtminstone årsungar tenderar ofta att röra sig i olika riktningar, bl.a. norrut (jfr. Zink 1981). Detta skulle delvis kunna förklara varför inga kontroller av kända västsvenska fåglar har gjorts vid Nidingens fågelstation, belägen på en ö i Kattegatt relativt nära mitt studieområde, trots att där gjorts relativt många fynd av svart rödstjärt. Kanske är det istället svarta rödstjärtar från Danmark eller Sydsverige som observeras på Nidingen under sensommaren? Den korta uppehållstiden hos många höstfåglar i Västsverige talar för att individomsättningen är hög, något som också försvårar studier av flockarna.

Flertalet av de revirhävdande hannarna försvinner redan under högsommaren. En del av dem genomför antagligen längre förflyttningar utanför undersökningsområdet och undgår därmed vidare upptäckt under hösten. I synnerhet de oparade, adulta hannar som redan under försommaren försvinner från sina revir, har fortfarande möjlighet att etablera sig framgångsrikt någon annanstans. Ett sådant exempel är en hanne som i april hävdade revir under tre veckor vid Ljunghusen i Skåne och som sjutton dagar senare kontrollerades vid Sundre på Gotland (Anonym 1981).

Hos ettåriga hannar som stannar kvar i området under hösten, kan spåras en koppling till deras tidigare revirstatus. Häckande 2K hannar är närvarande i högre grad än oparade 2K hannar. Hos äldre individer kunde jag dock inte belägga en sådan skillnad. En viss rörlighet förekommer såväl under höstmånaderna som mellan säsongerna, något som bekräftas av att 29% återfinns på nya platser under hösten. I Alperna uppvisar yngre och oparade hannar av svart rödstjärt en större förflyttningsbenägenhet. Några sådana samband går dock inte att fastställa i Västsverige då materialet är alltför litet. Andelen förflyttningar sker dock i samma omfattning i vårt utbredningsområde som i Alperna (Weggler 2000).

Utgår man från en beräknad dödlighet på 55,4% hos adulta fåglar (Erard & Yeatman 1967), återvände flertalet av hösthannarna till undersökningsområdet påföljande häckningssäsong. Majoriteten av dessa besatte då samma revir som de uppehöll sig i under våren året innan, och som delvis sammanföll med deras höstrevir. Weggler (2000) anger för Alperna att revirsituationen under hösten snarare påminner om kommande vår än föregående häckningssäsong. Hos de västsvenska hannar som försvann redan under sommaren, återkom avsevärt färre än bland höstfåglarna och hälften av dem hade då etablerat sig i ett nytt revir. Jämförelser mellan dessa båda grupper visar ingen större skillnad när det gäller ankomstdatum eller häckningsandel, medan däremot häckningsresultaten skiljer sig numeriskt på så sätt att höstfåglarna tenderar att ha högre häckningsframgång påföljande vår.

En bakomliggande orsak till svarta rödstjärtens revirbeteende under hösten kan sökas i årsungarnas uppträdande efter att de blivit självständiga. Många unga svarta rödstjärtar lämnar då födelseplatsen och företar längre förflyttningar innan de har genomfört sin kroppsruggning. Det rör sig främst om ungar från förstakullar som redan under högsommaren beger sig ut på längre s.k. ungfågelströvtåg (jfr. Otterlind 1954, Menzel 1983). En förhållandevis sen ruggningsperiod som infaller under augusti–oktober, ger utrymme för en sådan spridningsstrategi (Berthold 1983, 1985). Tidiga ungfågelrörelser bland tättingar är dåligt utforskade (Baker 1993), men finns beskrivet från Sverige hos bl.a. trastsångare, rörsångare, sävsångare och talgoxe (Ehrenroth 1976, Johansson 1980, Stervander 1999).

Svarta rödstjärtens sommarsträck är relativt väl dokumenterat jämfört med många andra arter. Ringmärkningsmaterial från Ottenby och Nidingens fågelstationer redogör för svenska förhållanden (Knutsson 1981, Andersson 1986). Från Mellaneuropa hänvisar Biber (1973) till studier i de schweiziska Alperna, där en markant sträcktopp av fåglar i juvenil dräkt noterades i skiftet juli/augusti. Zink (1981) anger flera fall där unga belgiska och tyskmärkta svarta rödstjärtar vid denna tidpunkt förflyttat sig, bl. a. i nordlig riktning, som längst en sträcka på 29 mil. Dessa strövtåg leder dem till nya platser där de kan genomföra den energikrävande ruggningen.

En stor del av individtillskottet i Västsverige under hösten kan sannolikt härröra från sådana ungfågelrörelser. De årsungar som iakttas i september uppvisar genomgående olika stadier av aktiv kroppsruggning (R. Andersson, opubl.). Fåglarnas uppträdande visar på stor opportunism, då de snabbt förmår uppsöka platser där stora mängder insekter samlats, exempelvis i hamnarnas timmerupplag. Där formerar de sig tidvis flockvis och kan dra nytta av ömsesidig information (skydd mot predatorer, förekomst av föda). Men sammanhållningen kan lika hastigt upplösas och nya konstellationer ta form på annat håll. Flera exempel finns där årsungar uppehållit sig på en plats, men senare under hösten återfunnits på nya lokaler, i ett fall nära fyra kilometer bort. Därmed uppstår en ökad konkurrens om viktiga resurser, speciellt födan, som redan i början av september förekommer betydligt sparsammare och mer klumpat än under häckningssäsongen.

Av de boungar som färgmärkts inom studieområdet var 10% närvarande under hösten, men de allra flesta hade då lämnat sina födelserevir. De sågs ofta bara någon dag på samma plats och var den individkategori som uppträdde rörligast. Det finns dock en påtaglig skillnad mellan första- och andrakullar, där tidigt flygga ungar svarar för de längsta rörelserna (jfr. Menzel 1983). Hur långt utanför undersökningsområdet årsungarna kan förflytta sig under denna årstid är ännu oklart. Återfynd av västsvenska årsungar föreligger under påföljande vår exempelvis i södra Norge, där en hona konstaterades häcka 25 mil från födelseplatsen (Steel 1993). Det är inte otänkbart att den rört sig dit redan under sensommaren och genomfört sin första ruggning där.

I Alperna ses hösthannar tillsammans med honor i uppvaktningsbeteenden liknande det på våren och samma par återvänder ofta och häckar ihop påföljande säsong (Weggler 2000). I Västsverige har sådana beteenden endast noterats ett fåtal gånger.

Sång och revirförsvar under hösten förekommer i mindre omfattning bland äldre hannar då de uppträder i flockar på födorika platser. Att successiva förflyttningar kan äga rum mellan sådana områden indikerar en hög flexibilitet. Höstsångens huvudsakliga funktion i vårt utbredningsområde förefaller vara att monopolisera viktiga födoresurser inom “hemområdet“. Tidigare erfarenhet och lokalkännedom bidrar till individuella fördelar även i ett bredare perspektiv, vilket torde öka överlevnadschansen och häckningsframgången påföljande vår.

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Summary

Autumn biology and song activity in a population of Black Redstart Phoenicurus ochruros *in south-western Sweden*

Introduction, material and methods

The Black Redstart is unusual among Swedish passerines, because it has a marked song period during autumn. The origin of the autumn song and its function has been discussed in different connections but the occurrence has seldom been studied in detail. In general, autumn song is thought to result in reproductive benefits during the following breeding season, especially among species which spend the winter in their breeding area (e.g. Hegner & Wingfield 1986, Logan & Hyatt 1991,Weggler 2000) The autumn biology of birds is not very well studied and in the Black Redstart the social structure, including autumn flock behaviour, is then of special interest.

To investigate the autumn biology and the function of the autumn song in a south-western Swedish population of Black Redstarts, the song activity, structure of the flock and origin of known individuals were studied. The study areas are located at the harbour of Gothenburg and adjacent factory environments, and also the harbour of Varberg with surrounding industrial environment. During the period 1 September to 20 November each year 1983–1997, the presence/absence of Black Redstarts was checked on average every fifth day (in 11 of the years) in a total of 45 known territories. During four years (1988, 1990, 1993, 1994) the study areas were visited more seldom, on average every 12 day. The territories were divided into 21 optimal and 24 suboptimal sites, according to an earlier classification of territories made during the breeding season. A scale ranging from 1–30 was used, and the optimal territories were estimated to correspond to 8–30 points (Andersson 1995).

The present study is based on 254 observations of males observed for a continuous period of at least 30 minutes (Table 1). Of these 254 observations, 69 consisted of colour-ringed birds (43 different individuals) and the remaining 185 observations were of unringed birds. At each observation song activity, accompanying individuals, territory fights, formation of flocks and social relationships were noted. To get a more detailed picture of the origin of the autumn birds and their breeding success the following spring, I carefully checked for previously colour-ringed birds. In total, the data set is based on 105 territorial adult males (2y or older), 20 adult females and 188 nestlings.

Song frequency is defined as number of song strophes per unit of time, whereas the conception song occurrence in this paper includes if song was heard at all from a male during a visit to the study area. A distance of ≥300 meters between the spring and the autumn “territories“ was considered to be a movement between seasonal territories. I define a flock as a gathering of birds appearing in dense (within 10–20 m) or lose (≤100 meters) groups. Playback of Black Redstart song from a tape recorder was sometimes used when catching birds, and also in a few instances for aggression tests.

Results

During 254 observations, males were heard singing at 165 occasions (65%). Of these were16 performed by yearlings which correspond to 10% of all song occasions (Figure 1). Some differences in song occurrence were found in relation to if the birds were alone or in a flock. Yearlings were more often heard singing in flocks, while adult males were singing more often when they were alone in their territories (yearlings: $\chi^2_{(1)}$=7.47, p=0.063, n=23; adults: $\chi^2_{(1)}$=4.51, p=0.034, n=37; Tab. 2). The majority of all males (83%) were found in optimal territories, whereas 17% stayed in suboptimal territories. 69% of yearlings (mean=14.2 territory points) and 86% of adults (mean=21.1 territory points) were found in optimal territories (Mann-Whitney U-test, p=0.015, n=23 yearlings and 37 adults).

In more than 50% of the 254 observations males were found to be alone. The rest were found in flocks of different size, often at sites with exceptional rich food resources (for instance stores of timber) (Table 2). The composition of flocks is shown in Figure 2. In these flocks, I found males that previously had been neighbours, breeding pairs and yearlings, but also an important share of unringed birds originating from outside the study area. Territory fights took place exclusively between neighbouring males at 3% of the 254 observations, but were never observed when they were together in flocks.

During springs, I located and colour-ringed 105 territorial males in my study area, and 34 (32%) of these had been located also during the autumn (Table 3). The remaining 71 males had disappeared already during the preceding summer (median value 26 June). The majority of the 34 males had previously been breeding in high quality territories. The correlation between their previous spring status and autumn presence were statistically significant in 2y males ($\chi^2_{(1)}$=8.93, p=0.028, n=55) but not in 3y+ males ($\chi^2_{(1)}$=0.33, p=0.56, n=50). The amount of time spent in the autumn territories varied between 1 and 70 days (mean 11.4 days), but more than 50% of the males were observed only one or a few days (Table 4). Eight of 20 breeding females (40%) were observed on average for 14.8 days in autumn (Table 3, 4).

Nineteen out of 188 (10%) coloured-ringed nestlings were located during autumn and they stayed on average 6.0 days at the same place compared to 11.4 for adults (Mann-Whitney U-test, p=0.012, n=19yearlings and 34 adults). Seventeen of the nestlings stayed only one day.

Movements between spring and autumn appeared in about 50% of the 61 birds present in autumn (Table 5). Many of them were found at sites with remarkable rich food resources. Ten out of the 34 males (29%) had moved to a new place, but most of them remained in their spring territories. The distance of these movements varied between 300 to 2000 meters (mean 780 meters). Three males moved gradually in autumn between several different territories. Among the 8 adult females, three had moved 300–700 meters (mean 530 meters), whereas the remaining five remained in their earlier breeding territories.

Seventeen out of 19 yearlings (89%) had moved from its place of birth to a new autumn site. The distance varied between 300 to 7000 meters, with an average of 1280 meters for first-broods and 360 meters for second-broods. Four of the yearlings stayed in different places during autumn.

Fifteen of the 34 autumn males (44%) returned to the study area the next spring (Table 6). Nine returned to the same territory as they had occupied the previous season. Six males had changed territories between spring and autumn. Of these, one was back on his autumn territory, whereas five returned to their previous spring territory. Fourteen (20%) of the 71 males that disappeared already during the breeding season returned the next year, compared to 44% of the males that held territories also in autumn ($\chi^2_{(1)}$=5.68, p=0.0172, n=105). The autumn-birds produced on average 5.2 fledged young/breeding pair, whereas the males only present the previous spring produced on average 3.7. However, these differences were not statistically significant (Mann-Whitney U-test, p=0.28, n=10 and 9). Of the birds that were present in autumn, one out of 19 yearlings and two out of 8 adult females returned the following spring.

Discussion

The autumn song of the Black Redstart in west Sweden reaches its peak in September–October. The majority of the males are found in good territories, and the adults with high song occurrence possessing territories of the highest quality. Yearling males produce song less often and it has more the character of subsong; according to Nicolai (1992a) it can be considered as a part of song learning. The autumn song in adult males is most often performed when they appear solitary on their territory, which is in contrast to yearlings that show higher song output when appearing in flocks. When food is concentrated and abundant (for instance at stores of timber rich in insects), many birds including adult males are found in flocks. During such behaviour song output and territory defence is reduced in adult males. Successive movements between such food rich sites indicate a high flexibility in autumn.

Formation of flocks is an important part of the autumn biology in this population of Black Redstarts. These flocks are casual formations with birds from the local area, birds from distant territories, and a large number of unknown individuals of which at least some come from outside the study area. The exchange rate of birds is high in these flocks.

There seems to be a connection between males who stay in the area during autumn and their territory status the previous spring. Breeding 2y males were more often present in autumn than unpaired 2y males. A certain degree of movements occurred over an autumn, as well as between spring and autumn seasons.

Assuming a mortality of 55.4% in adults (Erard & Yeatman 1967), most of the autumn males returned to the study area the following breeding season. The majority of them occupied the same territory as in the previous spring, and it partly coincided also with the autumn territory. In contrast, Weggler (2000) reports from the Swiss Alps that birds changed territories between spring and autumn, but then tended to stay in their autumn territories to breed the following spring. In my Swedish study area, males that disappeared already during summer had a much lower return rate than males present in autumn. These two groups of males did not differ in date of arrival or in the probability of forming a pair bond, whereas breeding success tended to differ.

A possible reason for the territorial behaviour in the Black Redstart during autumn may be found in the behaviour of yearlings after independence in autumn. Then, many young Black Redstarts leave their place of birth and undertake long movements, up to 290 km (Zink 1981), before they undergo their body moult. A late period of moult in August–October may facilitate such a dispersal strategy (Berthold 1983, 1985). These long movements of young birds take them to new places where they can perform their partial moult. A great deal of the surplus of individuals in western Sweden during autumn probably originates from such yearling movements, and this is likely to increase the competition over important resources.

The main purpose of song in autumn in this population seems to be to monopolize territories containing important food resources. Besides exclusive access to such food resources, the autumn territoriality also provides other advantages (e.g. local knowledge of sites and neighbours), which further will increase survival chances and may improve reproductive success the following spring.

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Weights of yolk body and hatchling in relation to the egg weight in the Treecreeper *Certhia familiaris*

ANDERS ENEMAR

Abstract

The weights of fresh eggs, yolk bodies, and hatchlings were measured during the period 1998–2000 in a Treecreeper *Certhia familiaris* population in a deciduous forest in south-western Sweden. The weight of the hard-boiled yolk body was positively and significantly correlated with the fresh egg weight among and within clutches. The same significant inter- and intra-clutch relations were also found between eggs and young nestlings (average age 12 hours) or fresh hatchlings, both with regression coefficients of a magnitude surpassing those of other investigated passerine species. The proportion of yolk weight tended to decrease with increasing egg weight, whereas the proportional weight of the hatchlings increased, showing a significant linear regression upon egg weight. The pronounced weight increase of hatchlings from heavier eggs strongly suggests a possible adaptive significance of the likewise pronounced intra-clutch egg weight hierarchy in the Treecreeper population studied.

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Introduction

The size and weight of eggs vary considerably between and within clutches in the Treecreeper *Certhia familiaris*. The eggs increase in weight in the laying sequence. This weight hierarchy was considered adaptive presupposing that the larger eggs give rise to larger or heavier hatchlings (Enemar 1997). Such a relation in all probability applies to the Treecreeper, as a positive egg/hatchling correlation has been demonstrated, albeit with varying accuracy, in all of the fourteen other investigated passerine species (for references, see Discussion). Most results are based on comparisons among clutches, whereas information on the egg/hatchling relation within clutches is scarce or non-existent. Knowledge of the latter relation is crucial for the interpretation of the significance of the intra-clutch egg weight hierarchy and was therefore included in this study, together with estimations of the egg/hatchling relations among clutches.

Opinions differ regarding to what extent the weight variation reflects a corresponding variation in the quality and composition of the egg. It has been demonstrated in a few species that the weight increase is mainly due to inclusion of more water (Bryant 1978, Ojanen 1983b, Clarkson 1984, Bancroft 1985) which may apply also to the hatchling (Clarkson 1984). As a matter of fact, there seems to be no consistent pattern in the relation between egg size and egg composition among passerines (Williams 1994). Thus, this study also focused on the relation between the weights of the egg and its yolk body, although the amount of yolk with its lipids provides only a coarse measure of the egg quality. However, a heavier hatchling may retain more yolk as a reserve (e.g. Bryant 1978, Rofstad & Sandvik 1985), which indicates at least one possible effect of the yolk mass variation to be considered when interpreting the meaning of the intra-clutch egg weight hierarchy

Methods

Hatchling weights of the Treecreeper were recorded during the springs of 1998–2000 in the Gunnebo recreational grounds outside the town of Mölndal in south-western Sweden. The investigated population breeds in artificial nest pockets (cf. Enemar 1992). A small sample of fresh eggs was collected in spring 2000 for estimation of the yolk weights.

The occupied pockets were inspected daily, mostly before noon, during the laying period to mark the newly laid eggs according to their laying order and to weigh them with the aid of a portable electronic balance (Bonso model-337) to the nearest 0.01 g. The nest visits were resumed during the days of hatching to weigh the hatchlings. Some nests were inspected several times a day to increase the prospect of discovering a single new hatchling, whose origin could be traced among the eggs. In order to evaluate the significance of age differences between the eggs and between the hatchlings when weighed, the daily weight change of some eggs was recorded before the start of incubation. The weight increase of a few hatchlings was followed during the first one or two days after hatching.

In order to study the weight relation between yolk and egg within clutches, two of the last laid eggs were taken from six nests before the beginning of full incubation, i.e. when the swelling of the yolk bodies had not yet started (cf. Enemar 1995). To increase the number of egg pairs, a six-egg clutch was used which was deserted immediately after laying. The two heaviest and lightest eggs were selected as pairs to be included in the analysis. (The number of collected eggs had to be kept at a minimum to avoid too heavy a toll on the reproductive output of the sparse population under study.) The eggs were boiled hard to facilitate a precise separation and handling of the yolk bodies which were weighed on the above-mentioned balance (cf. Muma & Ankney 1987). In order to be able to use the obtained measurements for investigating the variation pattern of the yolk mass in relation to the egg mass, it was presumed that the hard-boiled yolk bodies had all lost in weight in proportion to their fresh weights.

The statistical tests used are two-tailed: the parametric two-sample t-tests and regression (Bonnier & Tedin 1940), and the t-test for matched pairs (Fowler & Cohen, printing year lacking).

Results

The weight loss of eggs during the laying period

The weight loss of the first three eggs from clutches of five and six eggs was slightly more than one half per cent during the first day after laying (mean 0.64 ± 0.54 % (S.D.), n = 40). This corresponds to only 0.008 g of the mean weight of a fresh egg (1.26 ± 0.10 g, n=133 (Enemar 1997)), which may on average reduce the last figure of the weight measurements by about one unit only. Therefore the weights of the one day old eggs have been included in the analyses without adjustments, in the few instances (n = 7) when the laying start was not discovered until two eggs were present in the nest, i.e. on the second day of laying.

The initial increase of hatchling weight

The weight change of chicks that had hatched during the same day or the preceding night was followed during their first day as hatchlings. Fourteen young were checked over a total of 23 periods lasting from four to nine hours. The weight increase per hour was calculated, resulting in an overall mean of 0.023 ± 0.009 g (S.D.) (n=23). This figure was used when deriving the chick weight at the moment of hatching in cases when the weighing occurred several hours later.

Hatchling weight in relation to egg weight

All hatchlings of 39 clutches were weighed within 24 hours after hatching (average age 12 hours). A positive correlation was found between the clutch means of the hatchling weight and the egg weight (unhatched eggs excluded) ($y = - 0.54 + 1.28x$; $r = 0.731$; $n = 39$; $p < 0.001$).

Seventeen eggs from 14 of these clutches hatched during daytime and within inspection intervals of 12 hours or less. In these cases it could be established to which egg the hatchling belonged. The age of the hatchling was considered to be, on average, half of the interval between the inspections when hatching occurred. The weight was reduced accordingly to correspond to that at the hatching moment. The highly significant and positive correlation between the weights of these hatchlings and their eggs is presented in the diagram in Figure 1.

One chick from each of four clutches had just hatched with part of the egg-shell still attached to the body or left quite close when the nest was inspected. The weights (g) of these eggs and fresh hatchlings were as follows (hatchling first): 0.80/1.15, 0.86/1.21, 0.87/1.24 and 1.02/1.30. Also in this very restricted data set, was the relation between egg and hatchling significant and positive ($r = 0.95$; $n = 4$; $p = 0.05$).

The conclusion drawn from these analyses is that

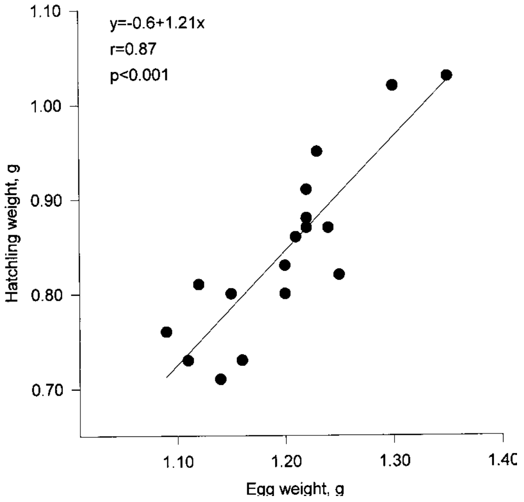

Figure 1. The relation between the weights of hatchling and egg. The hatchlings were weighed within 12 hours from hatching and the weights were adjusted to correspond to that of the moment of hatching using the mean weight increase per hour (see text).

Diagram som visar sambandet mellan vikterna för nykläckt unge (lodräta axeln) och dess ägg (vågräta axeln). De tyngre äggen kläcker fram tyngre ungar. Alla ungar har vägts inom 12 timmar efter kläckningen. Med hjälp av den kända medelviktökningen per timme för en unge under första dygnet har dess vikt i kläckningsögonblicket räknats fram.

heavier eggs produce heavier hatchlings at least when a sample of eggs from different clutches is analysed. A crucial question is whether this is also true for the egg/hatchling relation within clutches. This has been tested using intra-clutch pairs of hatchlings from identified eggs. Such pairs scarcely occurred among the 39 investigated clutches. Nine cases could be found with unequal intra-pair egg weights. Five pairs had the same interval, varying from 5 to 24 hours, between the last inspection of the egg and the first inspection of its hatchling. In order to increase the number of pairs, another four pairs were accepted despite the unequal inspection intervals of the siblings, varying from 3 to 12 hours. Thus, all siblings were very likely of different ages when weighed, but because of the many protracted intervals that included both day and night with their differing growth rates, no adjustments of the hatchling weights were made. A statistical test for matched pairs indicated that the heavier egg produces a heavier hatchling also within clutches (t-test: $t = 2.48$; $df = 8$; $p < 0.05$).

Yolk weight in relation to egg weight

The weights of 16 hard-boiled yolk bodies are plotted against their fresh egg weights in the diagram of Figure 2. A positive and significant relation between the yolk and egg weights is evident. The egg pairs from the same clutch are indicated by identical letters in the diagram. The result of a test for matched pairs is that heavier eggs also contain heavier yolk bodies within clutches (t-test: $t = 5.00$; $df = 7$; $p < 0.01$).

Discussion

The weight loss of the fresh egg

The declining egg weight observed during the first day after laying has been estimated in a small number of passerine species. The percentage values are all close to the weight loss of 0.64% shown by the Treecreeper egg: *Hirundo rustica* 0.4%, *Turdus migratorius* and *Quiscalus quiscula* 0.2% (Manning 1979), *Ficedula hypoleuca* 0.2–0.5% (Kern et al. 1992) and *Troglodytes aedon* approx. 0.5% (Styrsky et al. 1999). The only exception is *Parus caeruleus* with a mean weight loss of only 0.0008 g (0.07%) (Nilsson & Svensson 1993). This significant difference might be due to the habit of this species of keeping the eggs carefully covered with insulating nest material, which may reduce the water evaporation rate from the eggs when the female is away from the nest.

The daily weight loss of the eggs increases during the laying period, probably due to the successive

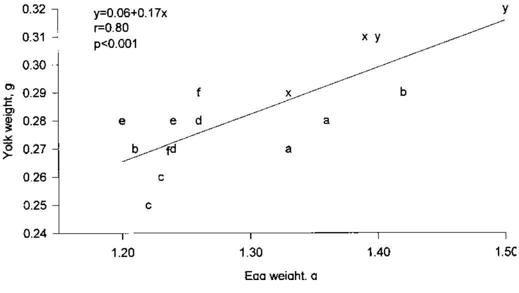

Figure 2. The relation between the weight of the hard-boiled yolk and the weight of the fresh egg. Identical letters indicate pairs of eggs from the same clutch.

Diagram som visar sambandet mellan äggets (horisontell axel) och dess gulas (vertikal axel) vikt. Som synes har de tyngre äggen också en tyngre gula. Diagrammet visar två ägg från varje kull vilka betcknas med samma bokstav.

increase in incubation attentiveness. Manning (1982) found a mean decrease in weight during the whole laying period of 0.9±0.08% for seven passerine species. The corresponding figure, calculated from 16 clutches of the Treecreeper, is 1.8±1.9% (n=57). The comparisons with other species thus indicate that the Treecreeper eggs suffer the greatest weight (water) loss during the days before the beginning of incubation. The explanation might be (1) that the eggs are small and of the same size as those of *P. caeruleus,* i.e. with a relatively larger surface area than those of the other species referred to above, and (2) that the clutch is left practically uncovered when the female bird is out.

The weight relation between egg and hatchling

The relation between the weight of the fresh egg and its hatchling has been studied in at least 15 passerine species including the Treecreeper. The parameters used are weight or volume of the egg, and weight or size of the hatchling. However, since the egg weight and volume are strongly correlated (Enemar 1997, with references) as are hatchling weight and size (e.g. Richter 1984, Rofstad & Sandvik 1987, Magrath 1992, Ward 1995), the choice of parameter has no significant impact on the calculations. It should be remembered, however, that larger eggs may give rise to heavier chicks due to a large yolk reserve rather than being structurally larger (Williams 1994). The studies differ as regards the amount and precision of presented data, and the analyses are based either on the weights of individual eggs and hatchlings within and among clutches or on the mean values of clutches. As it is troublesome to obtain enough data from hatchlings by following the hatching process closely in the field, sometimes the hatching of eggs brooded in an incubator has been studied. According to the results of these investigations, a positive relation between the weight or size of the passerine egg and the hatchling has been reported for *Parus major* (Schifferli 1973), *Quiscalus quiscula* (Howe 1976), *Iridoprocne bicolor* (De Steven 1978), *Molothrus ater* (Nolan & Thompson 1978), *Delichon urbica* (Bryant 1978), *Pica pica* (Clarkson 1984), *Xanthocephalus xanthocephalus* (Richter 1984), *Ficedula hypoleuca* (Järvinen & Ylimaunu 1984), *Corvus corone* (Rofstad & Sandvik 1985), *Empidonax minimus* (Briskie & Sealy 1990), *Turdus merula* (Magrath 1992a), *Parus caeruleus* (Nilsson & Svensson 1993), *Hirundo rustica* (Ward 1995) and *Troglodytes aedon* (Styrsky et al. 1999).

To my knowledge, apart from the late (second) clutches of *Troglodytes aedon,* which showed no correlation (Styrsky et al. 1999), no investigation has reported a lack of correlation between egg and hatchling weights. There seems, therefore, to be a general rule among passerine species that larger eggs give rise to heavier hatchlings. This holds at least for comparisons among clutches, although it is generally assumed, rightly or wrongly, that this egg/hatchling relation applies also within clutches, as shown above for the Treecreeper.

The adaptive significance of the egg size and its variation within and among clutches is still under debate (e.g. Nilsson & Svensson 1993, Stoleson & Bessinger 1995, Styrsky et al. 1999). As far as the intra-clutch variation is concerned, the egg weights normally increase in the laying sequence of the Treecreeper (Enemar 1997). As the incubation often starts before clutch completion with asynchronous hatching as a consequence, it follows that the largest eggs hatch last and that the hatchlings are heavier compared to the hatching weight of the siblings. In seven investigated clutches the mean weight of the last chick was 0.90 + 0.06 g on the day of hatching, which was significantly less than the mean weight, 1.17 + 0.13 g, of the earlier hatched siblings (t-test: $t = 6.08$; $df = 6$; $p < 0.00l$). The hatching weight “surplus“ of the last hatchlings has nevertheless been assumed to enhance the prospects of survival and therefore considered to be the selective force resulting in the egg weight hierarchy within clutches according to the “brood-survival“-hypothesis (cf. e.g. Slagsvold et al. 1984). However, this remains to be demonstrated in the Treecreeper.

Nilsson & Svensson (1993) remark that the slope of the regression of nestling weight upon egg weight is close to one in *Parus caeruleus* (regression coefficient $b = 1.01$). This means that every increase in the egg mass results in the same increase in the nestling mass. Their calculation was based on clutch means of eggs and nestlings aged 52 hours. In the Treecreeper the b-values exceed one in all calculations. It is 1.21 in the equation of Figure 1, 1.28 when the regression is based on 39 clutch means with mean nestling age of 12 hours, and l.42 for the above mentioned four chicks with hatching just finished. This indicates that the weight of the hatchling increases more than the egg weight, consequently resulting in an increasing relative weight. The quotient hatchling-weight/egg-weight, derived from the data sample in Figure 1, is significantly and positively correlated with the egg weight ($y = 0.23 + 0.40x$; $n = 17$; $r = 0.59$; $p < 0.02$).

Among the passerine species listed above, seven regression coefficients are reported (based on hatchling weights), which are all clearly less than one, ranging from 0.50 to 0.87. This indicates that the larger eggs of the Treecreeper are supplied with proportionally more nutrients to produce the most pronounced hatchling weight hierarchy among the investigated passerines.

The weight relation between the egg and its yolk body

Even if a positive correlation between the weights of yolk and egg is highly significant in the Treecreeper (Figure 2), there is no relative increase of the yolk body corresponding to that of the hatchling. The proportion of the yolk weight probably decreases with increasing egg weight. A test of the data presented in Figure 2 indicates a negative although insignificant relation ($r = - 0.39$; $n = 16$; $p < 0.2$). Available information regarding other passerine species is diversified, to say the least. A positive relation is found in *Parus major* (Schifferli 1973, Perrins 1996), with a negative trend of the relative yolk weight (Ojanen 1983a). Positive correlations are reported also for *Delichon urbica* (Bryant 1978), *Molothrus ater* (Ankney & Johnson 1985), *Agelaius phoeniceps* (Muna & Ankney 1987), and *Quiscalus major,* where the weight increase is said be due to inclusion of more water (Bancroft 1985). *Corvus corone* is special in that the relative yolk sac weight increases with egg weight (Rofstad & Sandvik 1987). No definite trends are found in *Sturnus vulgaris* (Ricklefs 1977, 1984), *Tyrannus tyrannus* (Murphy 1986), *Ficedula hypoleuca* (Ojanen 1983a), and *Parus caeruleus* (Kunz 1999). The relative yolk weight decreases with increasing egg weight in *S.vulgaris* (Ricklefs 1977) and *F. hypoleuca* (Ojanen 1983a).

Nevertheless, as demonstrated above, larger eggs seem to give rise to heavier hatchlings generally in passerines, but it does not follow that a larger yolk body is necessary for the weight increase. Although the yolk mass might be of decisive importance for the amount of nutritive reserve in the yolk sac of the hatchling, the total egg weight is the best indicator of the resources (calories, lipids, proteins) available to the embryo (Carey et al. 1980). Larger eggs with their relatively smaller yolk bodies contain proportionally more protein-rich albumen (Arnold 1992, with references), which might further the embryonic growth rate and/or weight increase. The proportionally smaller yolk bodies in the larger eggs also means that more space is available for the growing embryo. These relationships may reasonably apply also to the Treecreeper.

Concluding remarks

As documented in a previous study (Enemar 1997), the size or weight of the Treecreeper eggs increases significantly from first to last egg in the clutch, rising from 96 to 104 %, on average, when size is expressed as a percentage of the clutch mean. It was hypothesised that this tendency and ability of the female to successively increase her investment in the egg is of adaptive value from at least two aspects: 1. Under favourable breeding conditions when incubation starts before the clutch is complete and hatching becomes asynchronous, the then presumed increased weight of the last hatchlings increases the prospects of survival in competition with the older siblings (cf. Howe 1976, Rydén 1978). 2. Under constraining conditions, the mentioned quality of the female may enable her, at the expense of the successive increase in egg size and the early incubation start, to go on laying without gaps and to keep even the last eggs of a size and quality to give rise to viable and normally fit and synchronously hatched chicks (Enemar 1997). Moreover, Magrath (1992b) writes that “the tendency to lay relatively large eggs later in the clutch might be selected for in order to counter the effects of an increasing risk of unfavourable conditions“.

This study confirms that the heavier eggs are of higher quality, judging from their heavier yolk bodies, and that they produce heavier hatchlings, also proportionally, in the Treecreeper. The comparatively large span between the smallest and largest eggs within clutches and the even larger span between their hatchlings indicate that the intra-clutch egg size variation is instrumental in the breeding strategy of this double-brooded species. To save time and be able to produce several broods, females regularly start to incubate before the last egg is laid. This selects for the evolution of a distinct egg size hierarchy in the Treecreeper. However, the survival and fitness of small and large young early and late in the hatching row remain to be investigated. In fact, there are few studies that strongly support the view that egg size and offspring fitness are positively related in passerines (Williams 1994). It should also be remembered that there are other egg qualities of survival value that are not related to size, among them, for example, the concentration of maternal antibodies (Kunz 1999).

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Sammanfattning

Sambandet mellan äggets, äggulans och den nykläckta ungens vikt hos trädkryparen Certhia familiaris.

Inledning

I en tidigare uppsats (Enemar 1997) visade jag hur äggen i varje kull blir större och tyngre under värpningen förlopp hos trädkryparen. Som regel är de båda sist värpta äggen kullens största. Då betydelsen av detta förhållande diskuterades, förutsattes att de tyngsta äggen också gav upphov till de tyngsta ungarna hos denna art. Eftersom de sista äggen i regel också kläcks sist, skulle dess nykläckta ungar stå sig bättre i konkurrensen med de äldre kullsyskonen, bl.a. därför att de sista ungarna var försedda med en större matsäck i form av gula från tiden i ägget. Det fanns alltså alla skäl att ta reda på om dessa förmodade samband existerar i verkligheten. Det gällde då inte bara att utreda om de tyngre äggen kläcker ut tyngre ungar utan även om de tyngre äggen också har en tyngre gula. Dessa spörsmål har nu utforskats med metoder och resultat som redovisas i denna uppsats.

Metoder

Undersökningarna genomfördes i Gunnebo utanför Mölndal på det bestånd av trädkrypare som där bygger sina bon i speciella häckningsfickor av takpapp (se Enemar 1992). Värpningen följdes upp genom dagliga besök, då varje nytt ägg vägdes med en för fältbruk anpassad elektronisk våg, Äggen försågs med ett nummer motsvarande platsen i värpföljden. För vissa kullar vägdes de äldre äggen flera dagar under värpperioden för att utröna hur stor viktminskningen var per dygn.

Vid tiden för kläckningen återupptogs bokontrollerna för att väga de nykläckta ungarna. Ofta gjordes fler besök dagligen i förhoppning om att endast en nykläckt unge tillkommit efter föregående inspektion. Ungen kunde då skiljas ut från ev. tidigare kläckta syskon, eftersom varje nykläckt och vägd unge märkts med färgpenna på kroppen eller med nagellack på några klor. För en ensam nykläckt unge kan man därmed avgöra från vilket vägt ägg den härstammar. Fältarbetets mål var att erhålla många sådana fall där både äggets och dess nykläckta unges vikt kunde bestämmas. Ett antal ungars viktökning registrerades med timmars mellanrum det första dygnet för att bestämma den genomsnittiliga viktökningen per timme. Med hjälp av detta värde kunde en unges ungefärliga kläckvikt beräknas även om vägningen kraftigt försenats i förhållande till kläckningsögonblicket.

För studiet av gulornas vikt insamlades två ägg från sex bon. Till dessa fogades två par ägg från en nyligen övergiven kull. Äggens vikt registrerades i fält i samband med insamlandet. Efter det att äggen hårdkokats kunde gulan lätt skiljas från vitan och vägas.

Resultat

Under första dygnet efter värpningen minskade äggets vikt (genom avdunstning) i genomsnitt endast 0,008 g av sin medelvikt på 1,26 g, d.v.s. endast 0,64%. Hos 14 ungar ökade vikten under första dygnet genom tillväxt i genomsnitt 0,023 g per timme.

För 17 vägda ägg blev ungens kläckvikt känd antingen direkt genom vägning i nära anslutning till kläckningen eller efter korrektion av vikten i de fall då ungen vägts inom max. 12 timmar efter kläckningen. Som framgår av diagrammet i Figur 1 föreligger ett säkert samband mellan vikterna hos ägg och unge. Tyngre ägg producerar tyngre ungar. I fyra fall var de nykläckta ungarna alldeles färska vid vägningen, eftersom den ena äggskalshalvan fortfarande satt kvar på kroppen eller låg strax intill i boet. Även dessa ungar visar klart på sambandet, vilket framgår av följande viktpar i gram (ungens vikt först): 0,80/1,15; 0,86/1,21; 0,87/1,24 och 1,02/1,30. I nio fall kunde sambandet prövas inom syskonpar, alltså för ägg och ungar i samma kull. Resultatet blev att även inom samma kull gäller att tyngre ägg producerar tyngre ungar.

De tyngre äggen innehåller också en tyngre gula. Sambandet visas med diagrammet i Figur 2. Det innebär att de större och tyngre äggen också innehåller mer näring. Sambandet gäller också för äggpar inom en och samma kull. Detta kan också utläsas av diagrammet, där de två äggen från samma kull betecknas med samma bokstav.

Diskussion

Den viktminskning om drygt en halv procent som trädkryparäggen genomgår per dygn i avvaktan på ruvningsstarten, säkerligen genom avdunstning av vatteninnehållet, överensstämmer i stort med vad man funnit hos fyra andra tättingarter. Enda undantaget är blåmesen, vars ägg minskar med obetydliga 0,07% per dygn. Detta kan förklaras av att blåmeshonan så omsorgsfullt håller äggen täckta med isolerande bomaterial, då hon är frånvarande. Så sker ej hos trädkryparen, vars bobale innehåller obetydligt med fjädrar, ull eller annat värmeisolerande material.

För 14 undersökta tättingarter har det visats, att större eller tyngre ägg resulterar i tyngre ungar, ett resultat som oftast baserats på jämförelse mellan medelvärden för hela kullar. Inget undantag från denna “regel“ har så vitt känt hittills rapporterats. För trädkryparens del innebär det att den sist kläckta ungen från det stora och sist värpta ägget också är tyngst. I sju kullar kunde det konstateras att medelvikten för den nykläckta ungen var 0.90 g medan motsvarande vikt för de tidigare kläckta syskonen var 1,17 g och alltså hade ett försprång om 0.27 g eller 30%. Det är möjligt att den högre kläckvikten hos de sista ungarna hjälper dessa att klara den konkurrenssituation de kläckts in i, en rimlig hypotes som dock fortfarande är under diskussion.

Trädkryparen är unik i så måtto att den nykläckta ungens vikt ökar mer än vad man kunde förvänta av ökningen i äggvikt. Hos blåmesen ligger de båda viktökningarna ungefär i takt med varandra, medan hos sju andra tättingarter ungens viktökning släpar betydligt efter äggviktökningen.

En jämförelse med andra arter vad gäller sambandet mellan äggets och gulans vikt ger en minst sagt förvirrad bild. Exempel finns på samma förhållande som hos trädkyparen men även på frånvaron av samband eller på att gulevikten minskar, då äggvikten ökar. Även om trädkryparens gula ökar klart med äggvikten, så släpar den dock efter något, alltså tvärtemot vad som gäller för ungen. Man skall dock komma ihåg att det tyngre äggets ökning i äggvita inte är betydelselös. Denna är rik på bl.a. proteiner som främjar embryots tillväxt. (Dock finns forskare som påvisat att de större äggens viktökning beror endast på ett större vatteninnehåll, vilket i något fall skall gälla även för de nykläckta ungarna!)

Sammanfattningsvis, som tidigare visats har trädkryparen normalt en jämförelsevis stor skillnad mellan de tidigare lättare och de senare tyngre äggen i sina kullar. Denna skillnad är ännu större för motsvarande nykläckta ungars vikter. De sista tyngre ungarna har haft en tyngre gula till förfogande i ägget, vilket rimligen bidragit till tillskottet i ungens storlek och/eller vikt, det senare helt eller delvis i form av en rikligare gulereserv i tarmen. Vad allt detta betyder för trädkryparens fortplantningsframgång och de sist kläckta ungarnas överlevnadsmöjligheter kan inte avgöras i nuläget. Man saknar framförallt en jämförelse mellan de äldsta och de yngsta syskonens överlevnad till häckningsålder, något som ter sig minst sagt knepigt att utforska för en glest förekommande art som trädkryparen med sin tidiga häckning och sina regelmässigt(?) dubbla kullar.

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The occurrence of the Great Cormorant *Phalacrocorax carbo* in Sweden, with special emphasis on the recent population growth

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Abstract

The population of Great Cormorants *Phalacrocorax carbo sinensis* in Sweden has increased considerably in size during recent decades and currently Sweden holds about a quarter of the total Northwest European population. In 1999, the population contained an estimate of 25,600 pairs, distributed over about 154 colonies. The increase was particularly strong between 1986 and 1994 (mean annual increase 31%), and the population grew from 1800 to 15,500 pairs. After the mid-1990s, the population increase within most of the core area appear to have levelled off, while now fluctuating in size. However, in some northern breeding areas (including the coasts of Södermanland, Uppland, Gotland and several lakes) the population continued to grow at a high rate. With growing cormorant numbers, conflicts with human interests, mainly fishery, have increased. Hunting and egg pricking have frequently been used as methods to reduce cormorant densities locally and to solve fishery related problems. It seems, however, as these measures, in most areas, only have had limited effects in terms of stabilising or reducing population size of cormorants.

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Introduction

In many countries in Europe the Great Cormorant *Phalacrocorax carbo sinensis* became extinct in the 19th century or remained at low numbers (Zijlstra & van Eerden 1989, Lindell et. al 1995). In the early 1970s only a handful of colonies existed in the Netherlands, Sweden and Denmark and the total population in Europe consisted of no more than a few thousand pairs (Bregnballe 1996). However, due to several protective measures taken in various countries in the period 1965–1980 the population slowly started to recover. From about 1980 and in the following 10–15 years, populations of cormorants in several countries showed a spectacular population development with annual increases of 10–25% (Bregnballe 1996). From about the mid 1990s, the populations in the core areas of the Netherlands, Denmark, Germany and southern Sweden appear to have became saturated.

The return of the Great Cormorant has been so successful that renewed conflicts have come into existence in many areas. This has led to a pressure from, mainly, fishery organisations to reduce cormorant numbers. The main areas of conflict are related to (1) effects on natural fish populations leading to decreases in fishery yields (e.g. Keller 1995, Suter 1995b, Dekker 1997, Engström 2001), (2) predation and damage to fish in standing fishing gears (Bildsoe 1998, Engström 1998), (3) fish consumption at fish farms (Osieck 1991), and (4) effects on the vegetation at breeding and roosting sites.

In the management recommendations for the Great Cormorant in Europe, it is suggested that each country, or regional authority, should attempt to reduce these conflicts by local solutions (Anonymous 1997). In 1995, Sweden joined the European Community and the open hunting season on cormorants had to be abolished. Due to increasing conflicts between cormorants and mainly fishery interests, local authorities have in several areas decided upon widespread control actions during the last ten years. In addition to management practises approved by local authorities, a number of illegal actions against cormorants have taken place in the same period. However,

Cormorant colony (17 nests) at the islet Måsgrund close to the island of Svartö in southern Kalmars Sound, 1965. In total, 71 chicks were killed that year at the colony and the cormorants did not return to the islet the following year. Tage Olsson at a hide used for duck hunting (photo Edling Olsson).
Skarvkoloni (17 bon) på Måsgrund ca 1 000 m från Svartö i södra Kalmarsund 1965. 71 ungar dödades det året och skarvarna återkom aldrig mer till platsen. Skjutskåran användes vid andjakt. Fotot taget av Edling Olsson med fiskardrängen Tage Olsson i skåran.

despite the disputed value of present day management actions, no effort has been taken to evaluate the effects on local or national cormorant population sizes. Furthermore, no information exists on to what level management actions has solved or reduced fishery-related problems in Sweden.

The aim of this study is to give data on the population development of the Great Cormorant in Sweden, with special emphasis on the last fifteen years with rapid population growth and extensive geographical expansion. This paper also reviews the historical distribution of the cormorant in Sweden. Moreover, data on management practises to control cormorant numbers and illegal persecution are presented, and the roles of these actions are evaluated in relation to population development.

Methods

I gathered data on recent population estimates of the size of Great Cormorant colonies, mainly from local ornithologists. Annual number of breeding pairs are based on nest counts, usually at the peak breeding season. Normally, a group of nests was considered as a colony when separated by at least 200 m of water from other clumped breeding pairs. In rare cases, data from an established colony were missing in one year. In those cases, I chose a value in between the most immediate accurate sampling years. Data on management actions were collected from County Administration Boards, and data on illegal actions mainly from persons doing the inventories.

The geographical division of the data is based on provinces. Data from Lake Vättern, Lake Vänern, Lake Hjälmaren and Lake Mälaren (the four largest lakes of Sweden) are treated separately. Data on cormorant historic distribution were collected from the literature.

Results

Archaeological data

The history of the Great Cormorant in Sweden after the last glaciation has recently been examined by Ericson & Hernandez Carrasquilla (1997), and results from their study are summarised here. Cormorant remains, found at archaeological excavations, have been recorded from more than thirty places in southern Sweden, including the provinces of Bohuslän, Skåne, Blekinge, Öland, Västergötland, Gotland and Uppland. The oldest bone remains are ca 9000 years old. Some of the remains are from nestlings and juveniles (i.e. from Öland, Gotland and Uppland) which indicates the existence of breeding populations at that time. Based on bone sizes, the prehistoric Baltic cormorants appear all to have belonged to the nominate subspecies (*Ph. c. carbo*).

Recent history

In the literature, the presence of cormorants in Sweden was mentioned, probably for the first time, in 1555 (Olaus Magnus). Possibly, cormorants (*sinensis*?) bred in Sweden at that time. Later, in the 1690s, the famous naturalist Olof Rudbeck the Younger observed cormorants on several occasions at an expedition to northern Sweden (Brusewitz 1985). A cormorant in breeding plumage was also shot by this expedition in the Bothnian Bay. Neither Olof Rudbeck (1660–1740) nor Linnaeus (1707–78) mentioned any presence of breeding cormorants from their journeys in Sweden, and most likely, cormorants did not breed in Sweden during the 17th and 18th centuries.

In the 19th century, cormorants are known to have inhabited some lakes and coastal areas in the provinces of Skåne and Blekinge (Ekman 1922, Andersson et. al 1984 and references therein). In Blekinge, colonies were known from Saltärna (Ronneby archipelago), Dragsö (Hoby parish) and Tromtö (Karlskrona), and possibly they bred also at other sites. It is unknown when cormorants became established in Blekinge, but probably it occurred in the early 19th century. The distribution of cormorants in Skåne seems to have been somewhat more restricted than in Blekinge, and colonies are only known from Lake Krageholm and Lake Snogeholm. The colony at Lake Krageholm probably became established some time during the early 1870s. The total population within Skåne, and possibly also in Blekinge during the 19th century, most likely was small, breeding irregular, and never included any large concentrations similar to present day levels. For example, the colony at Lake Krageholm contained some 50 pairs after some years of existence. Two *Ph. c. sinensis* shot at Lake Krageholm in April and May 1881 (stored at Lund Zoological Museum) suggest that breeding cormorants in Skåne and Blekinge belonged to the subspecies *Ph. c. sinensis*. At Lake Krageholm, and probably Skåne as a whole, the cormorants seem to have disappeared at around 1881 due to destruction of nests and hunting (Neander 1918). However, Ekman (1922) mentioned breeding at Lake Krageholmssjön still in 1887. When the cormorant disappeared as a breeding species from Blekinge is unclear, but colonies may have existed until the early 20th century. Information from Vagnsö (Hoby parish, Blekinge) (Neander 1918) suggests that cormorants may have bred there in the cavity of an old oak-tree until 1909. Nevertheless, probably no breeding occurred in Sweden after 1909, at the latest, and the cormorant did not reappear as a breeding species in Sweden until the late 1940s.

Present distribution

The current distribution of Great cormorants in Sweden, as presented below, covers the period from the 1940s through 1999. Some data are also given for 2000. If not otherwise stated, population size data are from 1999. The number of breeding pairs for the different regions are presented in Table 1 and colony sizes in Table 2. Table 3 shows the number of disturbed and deserted colonies per province. Legal disturbance of colonies usually means egg pricking while illegal disturbance smashing of eggs, nest destruction and killing of young. The size distribution of deserted colonies is presented in Table 4 and the number of shot cormorants reported to the County Administration Boards is shown in Table 5.

Status in different provinces

Bohuslän and Halland

Along the Swedish West Coast cormorants commenced breeding in 1995. Three small colonies are currently known to exist: Flatskär (Askims fjord, Bohuslän, 70 pairs), Soteskär (Bohuslän, 7 pairs) and Vendelsöarna (Halland, 58 pairs). Unsuccessful breeding attempts are known also from three other places during 1990s. Fishery related conflicts is a growing problem along the West Coast, mainly due to increasing concentrations of non-breeding birds at summer, and over-wintering birds throughout the

Table 1. Number of breeding pairs (nests) of Great cormorants *Ph. carbo sinensis* per year and province, separated on lakes and coast, in Sweden 1948–1999. The far right column (%–99) shows proportion of pairs within each area. *Populationsutveckling, antal par (bon), för mellanskarv i Sverige 1948–1999. Kolumnen längst till höger visar andelen par per område.*

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	%-99
Lakes *sjöar*																
Halland*										6	1	1	?	?	0	0,0
Skåne**							107	483	842	1098	1007	1009	1305	1186	1312	5,1
Småland***										10	5	15	45	88	98	0,4
Östergötland****								16	150	211	334	532	668	953	1099	4,3
Västergötland			1	3	4	6	6	9	14	27	100	125	90	126	206	0,8
Lake Vättern										10	12	38	53	180	325	1,3
Lake Vänern					10	22	48	122	206	272	409	579	797	958	1094	4,3
Lake Hjälmaren												23	118	163	388	1,5
Lake Mälaren										4	32	60	79	185	379	1,5
Total inland (lakes)			1	3	14	28	161	630	1212	1638	1900	2382	3155	3839	4901	19,2
Charge on %				200	367	100	475	291	92	35	16	25	32	22	28	
Coast *kust*																
Bohuslän											26	30	?	4	77	0,3
Halland												3	?	40	58	0,2
Skåne							3	143	680	1028	1234	682	479	663	793	3,1
Blekinge	1		7	69	183	350	543	700	650	1280	1761	1727	1233	1584	1389	5,4
Öland					10	62	?	14	12	199	519	522	?	?	12	< 0.1
Småland	1785	1861	2452	3098	3927	3878	4577	6654	6468	6841	5964	7443	5846	7027	8403	32,9
Östergötland				280	446	950	1064	1128	1905	2746	2573	2165	1818	1621	1852	7,2
Gotland								85	390	1005	1035	1221	1776	2587	2943	11,5
Södermanland					50	174	263	125	425	664	362	1615	2175	2389	3016	11,8
Uppland									30	100	290	332	573	1092	1422	5,6
Gästrikland	Småland													70	0	0,0
Hälsingland	1948	1955	1960	1965	1970	1975	1980		17	32	0	0	12	5	0	0,0
Medelpad	probable breeding	75	?	125	175	337	753						22	38	87	0,3
Ångermanland										3	2	137	300	451	615	2,4
Västerbotten															9	< 0.1
Total coast	1785	1861	2469	3447	4616	5414	6450	8849	10577	13898	13766	15877	14234	17571	20676	80,8
Change on %		4	33	40	34	17	19	37	20	31	-1	15	-10	23	18	
Total coast + lakes	1785	1861	2470	3450	4630	5442	6611	9479	11789	15536	15640	18226	17389	21367	25577	100
Total change in %		4	33	40	34	18	21	43	24	32	1	17	-5	23	20	

*Ottersjön; **Ellestadsjön, Vombsjön, Ringsjön, Rössjön och Ivösjön (+4 lakes with occasional breeding); ***Salen, Läen, Vidösten, Bolmen, Kösen, Möckeln och Virstadsjön;

winter, which are blamed for consuming large amounts of fish. The colonies of Flatskär and Vendelsöarna have been subjected to human persecution. (Data from: Tommy Järås, Jan Uddén, and Anders Hultfelt).

Skåne

The cormorant re-established in Skåne in 1991. Colonies were founded both along the coast and in freshwater. In 1999, coastal colonies were situated at Eskilstorps holmar (543 pairs) and Gråen (250 pairs), both in Öresund Strait. Six freshwater colonies exist, of which the largest are located at Lake Ellestadsjön (708 pairs), Lake Ivösjön (410 pairs in 2000) and Lake Ringsjön (173 pairs). All major colonies (except for Ringsjön) appear to have stabilised in size. Conflicts with the commercial fishery are pronounced in several of the lakes. Still, human disturbance has been low at the majority of the breeding sites. (Data from: Gunnar Andersson, Patric Carlsson, Hans Cronert, Greger Flyckt, Pauli Kananen, and Nils Kjellén).

Blekinge

By far, the largest colony in Blekinge is located at Fröstensskärv (Ronneby) and contained 1613 pairs in 2000. The colony established in 1987 and its peak size was reached in 1995. The island of Fröstensskärv is leased from the private landowner by the Swedish Ornithological Society to secure undisturbed breeding conditions for the cormorants. Small colonies are found also at Eneskärvet, Karlshamn (17 pairs) and Annaskär, Torhamn (20 pairs). Illegal disturbance has occurred at several of the colonies in Blekinge. In an attempt to hinder settlement of new colonies at some islands, potential nesting trees and shrubs have been cut down and sheep allowed to graze. It seems as if these actions have been successful in terms of reducing or hinder breeding at these islands. For unknown reasons the eastern part of

Table 2. Number of commorant colonies, per colony-size category and province/lake in Sweden in 1999.
Antal skarvkolonier per kolonistorlekskategori i Sverige 1999.

	1–10	11–100	101–500	501–1000	>1001	Total
Lakes *sjöar*						
Skåne	1	2	3	1		7
Småland	3	2				5
Östergötland	2	5	5			12
Västergötland	2	1	1			4
Södermanland	1			1		
Lake Vättern	1	3	1			5
Lake Vänern	2	11	1	1		15
Lake Hjälmaren	2	6	1			9
Lake Mälaren	6	8	1			15
Total	20	38	13	2		73
%	27	52	18	3		100
Coast *kust*						
Bohuslän	1	1				2
Halland		1			1	
Skåne			1	1		2
Blekinge	2				1	3
Småland	2	3	3	3	3	14
Öland		2			2	
Östergötland	2	8	5			15
Gotland				1	1	2
Södermanland	1	7	9			17
Uppland	1	4	5			10
Medelpad	1	1				2
Ångermanland	2	1	2			5
Västerbotten	1			1		
Total coast	11	30	25	5	5	76
%	14	39	33	7	7	100
Total inland+coast	31	68	38	7	5	149
%	21	46	26	5	3	100

A further 5 colonies probably exist of which breeding pairs are unkown (Gotland: 2, Öland: 1, Södermanland:1, L. Mälaren: 1).

Blekinge is only sparsely populated by cormorants, and the population appears to be well below carrying capacity. Overall, conflicts with the fishery appear to be small in the area. (Data from: Lars Carlsson and Lars Möllersten).

Småland

The cormorant re-established as a breeding species at the island of Svartö in Southern Kalmarsund in the late 1940s, after having been absent for more than 40 years. The exact year of establishment is unknown but breeding is indicated from 1948 when a flock of cormorants was observed by Bengt Berg near a heronry at Svartö (Berglund 1956). From 1951, ca 30 pairs are known to have bred at Svartö (Berglund 1958).

Currently, in terms of number of breeding pairs, the coastal area of Småland is the most important breeding area for cormorants in Sweden. In 1999, three colonies exceeded 1900 pairs and the total number of pairs attempting to breed comprised 8400 (34% of the total Swedish population). In 1999, a total of 14 colonies were found on the coast and five in freshwater. The freshwater colonies are all very small and included altogether 98 pairs.

Human disturbance is common at many colonies in Småland and has conveyed rapid changes in size of some colonies. Moreover, disturbances have also contributed to the extinction of colonies, and the dispersal of individuals over the area. For example, during the last fifteen years, no less than 17 colonies have been subjected to human disturbance, of which 10 illegally. Ten colonies have vanished due to illegal persecution while 13 (mainly small) colonies are thought to have been deserted, seemingly without any clear human disturbance. The most well known colony destroyed illegally by humans is the colony at the island of Gåsö in northern Kalmar Sound. The whole colony, consisting of ca 3000 pairs, was exterminated during the peak breeding season in 1993 by some local people who cut down all the nesting-trees at the island. Despite extensive human disturbance, the population in Småland as a whole appears to have remained strong and the population size has been fairly constant since 1992. The apparent stability in population size may partly be explained by the fact that two colonies with large numbers of cormorants have developed at islands (Norra Sandholmen-Svartö-Törnholmen and Svartingskär) where colonies have been undisturbed. Currently, management actions such as egg pricking are allowed at all colonies except for the protected sites at Kungsholmen, Norra Sandholmen-Svartö-Törnholmen and Svartingskär. During the period 1994–2000, a mean of 2065 cormorants were reported shot every year. (Data from: Roger Alman, Kjell Johansson, Sven Johansson, Tommy Larsson, Bo Lewander, Lars Lindell, Krister Wahlström and Åke Widgren).

Öland

The first documented breeding at Öland occurred in 1989. Until 1999, colonies are known from at least four sites. The largest colony developed at the small island of Marskär (Löt) and reached 510 pairs in 1996. However, at around 1996, the nesting trees at Marskär were cut down by the landowner, and since then only a few pairs have bred at the island. An accurate figure for the current population on Öland

Table 3. Great Cormorant colonies (includ. 13 solitary pairs) of Sweden 1985–1999. The table shows number of disturbed (legally/illegally) and deserted colonies per province/lake.
Kolonier av mellanskarv i Sverige (inkl. 13 solitärhäckningar) åren 1985–1999. Tabellen visar antalet störda (legalt/illegalt) och övergivna kolonier (pga mänskl. störning/utan synbar mänsklig störning) för respektive landskap/sjö.

Province/lake	Known colonies 1985–99	Colonies in 1999	Legally disturbed	Illegally disturbed	Deserted due to human disturbance	Deserted seemingly without any human dist.	Data lacking
Landskap/sjö	*Kända häckningar 1985–99*	*Kolonier 1999*	*Legalt störda*	*Illegalt störda*	*Övergivna pga mänsklig störning*	*Spontant övergivna*	*Närmare uppgift saknas*
Lakes/*sjöar*							
Skåne	12	7		2		4	1
Småland	8	5		1		2	1
Östergötland	14	12	1	4	2		
Västergötland	6	4		1		1	1
Södermanland	1	1					
Lake Vättern	5	5					
Lake Vänern	16	15	1	1		1	
Lake Hjälmaren	11	9	3	2	1	1	
Lake Mälaren	19	16	1		1		2
Coast/*kust*							
Bohuslän	3	2		1		1	
Halland	3	1		1		2	
Skåne	4	2				2	
Blekinge	5	3	1	3	1	1	
Småland	34	14	7	10	9	11	
Öland	4	3	1			1	
Östergötland	23	15	5	12	8		
Gotland	6	4				1	1
Södermanland	19	18	1		1		
Uppland	11	10		3		1	
Gästrikland	1	0		1	1		
Hälsingland	4	0				4	
Medelpad	2	2					
Ångermanland	7	5				2	
Västerbotten	1	1					
Total lakes	92	74	6	11	4	9	5
Total coast	127	80	15	31	20	26	1
Total lakes+coast	219	154	21	42	24	35	6

is not available but amounts probably to no more than some ten pairs. The low population density at Öland is a bit surprising considering the large areas of shallow water suitable for feeding on the eastern side of the island. One explanation for the small number may be the lack of suitable breeding islands. (Data from: Lars Lindell).

Östergötland

In Östergötland cormorants commenced breeding in 1988 at Hanskären (in the outer mouth of Bråviken). In the 1990s, colonies became established at a great number of places and the number of pairs attempting to breed increased rapidly. Along the coast, peak numbers were reached in 1994 (2746 pairs). With an almost exponential population increase of 49% per year for the period 1990–1994 the population then decreased (-7% per year) in the period 1995–1999. In 1999, the coastal population consisted of 1852 pairs distributed over 15 colonies. Freshwater colonies have continued to increase and reached 1099 pairs in 1999. Only one colony has exceeded 500 pairs (Lilla Järknö with 642 pairs in 2000), but within Lake Roxen, six colonies fairly close to each other contained 894 pairs in 1999 (521 pairs in 2000). The first freshwater colonies were founded in 1992 and presently colonies are known within four lakes: Lake Roxen, Lake Glan, Lake Sommen and Lake Tåkern. The colony at Lake Tåkern, 10 pairs in 1999, was first established in a quagmire but was abandoned at an early stage.

Table 4. Size distribution of cormorant colonies in Sweden 1985–1999 that have been deserted either by human disturbance or spontaniously.
Storleksfördelning hos skarvkolonier som övergivits spontant eller pga mänsklig störning 1985–1999.

No. of pairs *Antal par*	With disturbance *Med störning* N	 %	Without disturbance *Utan störning* N	 %
1–9	4	17	27	77
10–99	10	43	5	14
100–499	7	30	2	6
500–	2	9	1	3
Total	23	100	25	100

Conflicts with the fishery are pronounced, both in freshwater and along the coast. On the coast, more colonies have been subjected to human disturbance than elsewhere else in Sweden. For example, in 1994 (peak year) 55% of all breedings (1635 pairs) were destroyed, mainly by egg pricking, either legally or illegally. For the period 1994–1999, an average of 707 (24%) of all commenced breedings were destroyed. Reported shooting includes a mean of 254 (max. 551) cormorants shot per year (1992–1999). Recently, control measures have involved also freshwater colonies, and in 1999 and 2000, 2 000 eggs were pecked each year in Lake Roxen while shooting numbered 141 and 300 birds, respectively. In total, along the coast, illegal disturbances have occurred in at least 12 colonies resulting in the disappearance of 8 colonies. Legal disturbances have involved five colonies. In terms of breeding pairs, the southern part of the coastal area most likely contains a population below carrying capacity due to systematic human disturbance. This disturbance may possibly have contributed to the strong increase observed in southern Södermanland in recent years, where disturbance has been low. (Data from: Göran Andersson, Göran Hector, Lars Hedenström, Lars Gezelius, Viking Olsson and Lars Svensson).

Västergötland

The first colony founded inland (after the disappearance of the cormorant in the early 20th century) probably took place in Lake Ymsen in 1987. This colony contained ca 135 pairs in 2000. Currently, Lake Vänern is the stronghold for the species in Västergötland (see below). Recently, breeding attempts with small colonies are known also from Lake Hornborgarsjön (76 nests), Lake Fävren (possible breeding), Lake Torpasjön and Lake Åsunden. Probably no chicks were produced in any of these colonies in 1999. (Data from: Kjell Andersson, Nils Eriksson, Gerard Gautier, Henri Engström and Peter Fäldt).

Gotland

In 1992, cormorants re-established at the island of Lilla Karlsö with nests placed among breeding guillemots on cliff shelves. A second colony with nests placed in trees was founded in1995 at Laus Holmar at southeastern Gotland. Small ground breeding col-

Table 5. Number of shot cormorants reported to County Administration Boards in Sweden 1992–2000. Hunting also occurred at Lake Glan but figures not available.
Antal skjutna skarvar rapporterade till länsstyrelserna 1992–2000. Jakt förekom även vid Glan, men siffror ej tillgängliga.

Year	Coast Bohuslän	Coast Blekinge	Coast Småland Öland	Coast Östergötland	Coast Uppland	L. Krageholmssj., Ellestadsj.	Lake Ivösjön	Lake Roxen	Lake Hjälmaren	Lake Mälaren	Totalt
1992			?	132							132
1993			?	229							229
1994			788	107							895
		95–99:					95–99:				
1995		<10/year	1740	157			200 (tot.)				1897
1996			2915	176		132		2			3225
1997			2296	no permit				few			2296
1998	153		2739	439				few			3178
1999	100		1548	541	111			141	554		2895
2000	82		2430	478	112			300	511	33	3864

onies also existed (1998) at Northern Gotland: Avagrunn (7 pairs) and Askugrunn (60 pairs). At the two main colonies, population increase has been strong in recent years although the colony at Lilla Karlsö now shows signs of levelling off. The Lilla Karlsö colony contained 2268 pairs in 2000 and that at Laus Holmar 1120 pairs in 2000. Both colonies are situated within protected bird areas. (Data from: Stellan Hedgren, Björn Hjernqvist and Kjell Larsson).

Södermanland

In recent years coastal populations in Södermanland have increased considerably in size and during the period 1995–1999 the number of breeding pairs increased by 74% annually. The total number along the coast included 3016 pairs distributed over 18 colonies in 1999. Conflicts with the fishery appear to be low in the area. Disturbance (legal) is known only from one colony. Most colonies are of medium size and no colony exceeded 500 pairs in 1999. Inland colonies exist at Lake Mälaren (see below) and Lake Näsnaren, Katrineholm (15 pairs in 2000). (Data from: Åke Andersson, Henri Engström, Björn Lundberg, Agne Swenzén and Bengt Söderlund).

Uppland

In the province of Uppland cormorants breed only at scattered localities. Cormorants established for the first time in the area in 1993 and the area is not saturated. Current colonies are concentrated in two main areas. In the south: Svartlögafjärden – Gälnan – Furusundsleden (five colonies) and in the north, Lövsta and Gävle Bays (three colonies). In between these two areas at least two small colonies exist east of Hargshamn (Galtfjärden) but parts of the area are not very well censused. The coastal colonies have increased with an average of 77% per year during the period 1995–1999. The three most northern colonies in Lövsta Bay and Gävle Bay were all subjected to severe human persecution in 1999, and production of young was probably close to zero at these colonies. In the northern area conflicts with the fishery is currently intense and fishermen blame both cormorants and seals to cause damage to the fishery. About 1400 pairs initiated breeding in Uppland in 1999. (Data from: Martin Amcoff, Henri Engström, Lars Gustavsson and Roland Staav).

Gästrikland

One colony initiated breeding on the island of Klubbstenarna in 1998 (70 pairs) but failed to produce any young. This failure was most likely due to human persecution. No breeding attempts are known from the area in 1999. (Data from: Per Aspenberg).

Hälsingland

Occasional breeding is known at four islets (Fisket, Storhällen, Korvgrund, Remmarharet) during the period 1993–1998. For unknown reasons, the cormorants have failed to establish permanent colonies within the area. The colonies were all very small and never reach more than a few pairs each. (Data from: Mats Axbrink).

Medelpad

The first documented breeding occurred in 1993. Currently two colonies exist at Rödskäret (Tynderöd parish, 82 pairs) and Skallandsskäret (an islet near Rödskäret, 5 pairs). (Data from: Lars Olausson).

Ångermanland

Breeding is known from at least seven sites during the period 1994–1999. The two largest colonies at Gnäggen (282 pairs) and Långskärsklubb (301 pairs) are found on rocky islets surrounded by fairly deep water. (Data from: Kurt Holmqvist).

Västerbotten

One colony consisting of nine pairs established on a rocky islet (Römselögrundet) in 1999. No breeding occurred at this site in 2000. This colony probably was the most northern breeding site ever for *Ph. c. sinensis* in Sweden. (Data from: Urban Grenmyr). However, in 2000, a colony holding 31 pairs was established in Finland in the far north of the Bothnian Bay. Most likely these cormorants belong to the *sinensis* subspecies (Timo Asanti, Finnish Environmental Institute, pers. comm.).

Status in major lakes

Lake Vänern

Lake Vänern is the largest lake in Sweden (570,000 ha). In 1989, cormorants established for the first time at the small islet of Ruskskär near Lurön. Currently (2000), 17 fairly evenly distributed colonies containing 1140 pairs are found over the lake except in the north-eastern part (i.e. Dalbosjön). All colonies but one are small and consist of less than

150 pairs. The largest colony is situated on western Kållandsö (620 pairs) and is the largest genuine freshwater colony in Sweden. The population increase of Lake Vänern has declined from a yearly average of 99% in 1990–1994 to 33% in 1995–1999. Conflicts with the fishery are intense in many parts of the lake, particularly in the south-eastern part. Bite-marks on fish inflicted by the cormorants in fyke and gill nets are common problems. However, reports of human disturbance at colonies are few. In an attempt to locally reduce cormorant breeding output, and thus damage to the fishery, local authorities in collaboration with fishermen and ornithologists treated eggs with paraffin oil at the colony of Dagskär, Kinneviken, in 1999 (Landgren 2000). The effort, which also included a follow-up of other bird species and neighbouring cormorant colonies, will be evaluated first within a few years time. (Data from: Thomas Landgren).

Vättern

Cormorants started breeding in Lake Vättern in 1994 at the rocky islet Jungfrun. The colony decreased from 25 pairs in 1999 to one pair in 2000. Currently, the largest colony is located at the island of Erkerna in the outer Motala Bay and nests are placed in mature forest. The colony held 220 pairs in 2000. In 1999, a total of five colonies were found in Lake Vättern of which three colonies were situated in the Motala Bay area and two colonies in the very northern part of the lake. Conflicts with the fishery appear to be low in the area and there are no reports of any human disturbance within any of the colonies. (Data from: Lars Gezelius and Ola Strand).

Hjälmaren

Cormorants settled in Lake Hjälmaren in 1996. The population increase was rapid, and in 1999 the population consisted of 388 pairs distributed over nine colonies. All colonies except one (Pjukstenarna, 172 pairs, 2000) contained less than one hundred pairs. At the moment, conflicts with the fishery are intense and damage to fish in fishing gears is the largest problem. Five colonies have been subjected to human persecution of which two illegally. In autumn 1999, fishermen and hunters, with permission from local authorities, organised common hunting with the aim of reducing the overall number of cormorants. Hunters were spread out over large parts of the lake, including islets and popular roosts, and altogether 554 cormorants were shot. This large-scale hunting procedure was repeated in 2000, this time involving more than 100 hunters at each time during three occasions. With the same hunting pressure 242, cormorants were shot on 21 August, 80 cormorants on 28 August and 61 on 1 September. In total 750 birds were allowed to be shot in 2000. The hunters noted that the cormorants behaved differently at the three hunting occasions, e.g. some cormorants were very shy whilst others were not, indicating birds of different origin. This hypothesis of different origin was confirmed also by ringing recoveries. (Data from: Ola Strand, Bo Andersson).

Mälaren

Cormorants commenced breeding in Lake Mälaren in 1994 and the population reached 379 pairs in 1999. The colonies show many similarities with those of Lake Hjälmaren. For example, cormorants nest only in trees and the colonies are distributed over many (16) and small colonies. The largest colony is situated at the island of Grönsö and contained 110 pairs in 1999. Human disturbance has not been documented in any of the colonies. However, the nesting-trees were cut down on the small island of Bogstenen (Galten) where three pairs bred in 1998. The cormorants did not return to the site in 1999. Legally organised hunting (cf. Lake Hjälmaren) was carried out in late August to early October 2000 at six occasions, and a total of 33 birds were shot (300 birds were allowed to be shot) (data from: Gillis Aronsson, Thomas Pettersson, Roland Staav and Pekka Westin).

Discussion

Historic populations

Archaeological data indicate that the Great Cormorant has a long history in Sweden and inhabited the Baltic region since the last ice-age. Although the precise geographical distribution and the numerical abundance of these cormorants cannot be determined, it is highly probable that the populations seen today are larger and cover a wider area than at any time before. When the former breeding subspecies *Ph. c. carbo* became extinct and replaced by present day *Ph. c. sinensis* is unknown, but the youngest remains of *Ph. c. carbo* found at archaeological excavations are from ca 800 – 975 AD (nestlings) and for adults ca 1300±50 AD (Ericson & Hernandez Carrasquilla 1997). It seems therefore to me that breeding populations of *carbo* must have become extinct at the earliest around 1000 AD, and no later than ca late 1600 AD. The cormorants observed (and also shot) by Rudbeck in the late 17th century most likely were *Ph. c. carbo*, coming from the coast of Barents Sea or the White Sea where this subspecies breeds. The occurrence of breeding *Ph. c. sinensis*, for the first time in the early 19th century, indicates a minimum time period of at least 100–200 years when most likely no cormorants bred in Sweden.

In the early 19th century *Ph. carbo sinensis* became established probably for the first time in Sweden. Cormorants established also in Denmark around this time (Jespersen 1949 in Berglund 1958). In the 19th century the population of *Ph. c. sinensis* of southeastern Sweden appears to have been small. Did the low population size depend on natural limitations or was the population kept low by hunting and/or human persecution? That question cannot safely be answered, but according to e.g. Nilsson (1858) and Neander (1918) (some) people hosted a very negative attitude towards the birds, and actions against the cormorants appear to have been frequent and organised. For example, the colony at Lake Krageholm disappeared in the early 1880s due to human persecution (Neander 1918). Probably, the population was prevented from expanding due to repeated hunting and human persecution. At a European level, most of the few existing colonies during the 19th and early 20th century in the Netherlands and Denmark were subjected to human persecution (Zijlstra & van Eerden 1989; Gregersen 1989). Although the existing information being fragmentary, human persecution presumably was an important factor in determining cormorant number and distribution, and probably also was the main factor responsible for the disappearance of the cormorant as a breeding species in Sweden sometime in the late 19th or early 20th century.

Recent population development

The recent history of the cormorant in Sweden begins at Svartö in southern Kalmar Sound where cormorants became established in the late 1940s (Berglund 1956, 1958). How the colony was founded has been debated, and it has been proposed that the colony resulted from an introduction of cormorant eggs taken from Denmark and placed in heron nests at Svartö. However, since no evidence seems to exist for this theory, other than oral reports, it is more realistic to think that the cormorants established spontaneously at Svartö. The latter explanation is supported by a correspondence in time with the founding of Svartö (and Danish cormorant colonies) and large numbers of cormorants driven away from a colony at Rügen in Germany during the 1940s (Jonsson 1977).

The cormorant colony of Svartö remained small for a long time. The slow increase of the colony may partly be explained by hunting, and every year about a third of the cormorants at the colony were shot (Edling Olsson pers. comm.). The hunting came to an end in 1965, when the manor got a new tenant who was less hostile towards the cormorants (Edling Olsson pers. comm.). Interestingly, also after hunting at Svartö had ceased, the rate of population increase continued to be low for more than a decade, and obviously other factors than hunting must have been responsible for the slow increase of the colony. Also the colony at Gåsö in Northern Kalmar Sound, establish in the early 1960s, remained small for more than two decades before it went through a rapid population development. Until 1986, Svartö and Gåsö were the only cormorant colonies in Sweden. A dramatic change in the population development occurred at around the mid 1980s when the population suddenly increased dramatically in size. For example, between 1986 and 1987, the population rose by 33% and new colonies were founded in Blekinge, Västergötland, the year after also in Östergötland, and at several sites in Småland (Tables 1 and 2). The population increase continued to be high until 1994 (mean annual increase 31%), but then the population in the core areas started to fluctuate about an even level. The observed increase in the total population size occurring after 1994 can to a large extent be ascribed to an increase in several of the inland lakes, at two sites at southern Gotland and the establishment of colonies along the coast from Södermanland and northwards. During the period of exponential increase (i.e. 1986 to 1994) the number of pairs increased from 1861 to 15,536 pairs (Table 1). During the same time period, the number of colonies increased from two to forty-six. Little is known about the mechanisms behind colony formation. However, in general, it is obvious that new colonies formed long before “core“ colonies were saturated, and sometimes at a long distance from the colony of origin. At about 1994, cormorants had reached most of its present range.

Present population

The current (1999) number of great cormorants breeding in Sweden comprises 25,200–26,000 pairs distributed over ca 154 colonies. This means that

Sweden currently holds about 25% of the total northwestern European population of *Ph. c. sinensis*. Except for Sweden, the main countries of northwestern Europe holding large cormorant populations include Denmark (42,000 pairs), the Netherlands (20,000 pairs) and Germany (15,000 pairs) (in 2000). Countries holding smaller, but increasing populations, include Poland (ca 14,000 pairs), the Baltic States (ca 7,400 pairs) and Finland (336 pairs) (in 2000). During the 1990s the population size within the core areas of the Netherlands, Denmark, Germany and southern Sweden seem to have reached an upper limit, and now fluctuate in numbers.

The present distribution of the breeding population of the Great Cormorant in Sweden is more or less contiguous along the whole south Swedish Baltic Sea coast from Blekinge in the south to northern Södermanland in the north. From Uppland and northwards there are large gaps in the distribution and most colonies are small. The reason for the low abundance along the Bothnian Gulf coast (<3% of the total Swedish population) may be linked to unfavourable foraging conditions and climate. In the early 1990s, cormorants attempted breeding on at least fifteen sites along the Bothnian Gulf, but only two colonies grew to considerable size (ca 300 pairs each), whereas seven colonies disappeared after only some years of presence.

For unknown reason the Swedish west Coast has not been inhabited by other than some few and small colonies. This is a bit surprising since large number of cormorants use the area for feeding during the winter (Bengtsson 1999). The absence is probably not related to marine salinity because *Ph. c. sinensis* obviously breed successfully in the marine environment in Denmark.

Cormorants settled inland, probably for the first time in 1987. During the 1990s growth and dispersal of inland populations have been rapid. For example, in 1995, 12% of the total population bred in lakes versus 19% in 1999. The cormorants seem to prefer the larger lakes, and currently, 45% of the inland colonies are located in the four large lakes of Sweden: Vättern, Vänern, Hjälmaren and Mälaren. Other important breeding areas include lakes at Skåne (27%) and Östergötland (22%). No inland colony is known to exist north of latitude 60°N, probably partly because of the long period of ice-cover which makes it difficult for the birds to accomplish the long breeding cycle. Colony size differs much between areas. The largerst colonies (1 500–3 000 pairs) are found in Blekinge (1), Kalmar Sound (3) and on Gotland (1). The largest colony in Europe, located at Katy Rybackie Gulf of Gdansk, contained ca 8000 pairs in 2000. The main factor determining colony sizes is probably related to the productivity and amount of food available to the cormorants near the colonies (van Eerden & Gregersen 1995). Human disturbance may also affect colony size.

The total number of Great Cormorant colonies known to have existed during the last fifteen years amounts to 215. At least thirty-five of these colonies are thought to have been deserted seemingly without any clear human disturbance. Most (77%) of the colony sites that have been abandoned spontaneously had less than ten breeding pairs (Table 4), and usually cormorants bred at the site only for a few years, at most five years.

Factors behind the population development

Several factors are though to have contributed to the recovery and strong increase of *Ph. c. sinensis* during the last decades. For example, recent studies indicate an exceptional high survival of immature and adult birds during the period of strong increase (i.e. 1970–1990), and in Denmark it was shown that first year survival was much higher (0.42–0.75) than for the fairly stable population of *Ph. c. carbo* breeding along the Norwegian coast (0.19–0.38) (Frederiksen & Bregnballe 2000).

The success of the Great Cormorant in Europe shows many similarities with the closely related and equally successful Double-crested Cormorant *Phalacrocorax auritus* of North America (Hatch 1995). Protection is thought to have played a central role, and the European population of *sinensis* began to increase after the species had been protected in the Netherlands in 1965. In Denmark the cormorant was given partial protection in 1971 and full protection in 1977. In 1980, the Great Cormorant was given full protection in all the member states of the European Union according to the EU Birds Directive. In Sweden, before the EU association in 1995, there was an open hunting season from 21 August to 28 February. This hunting, however, probably had little effect on the population since a majority of the cormorants had left Sweden for their winter quarters at that time.

During the last century many aquatic systems have been strongly influenced by human activities, such as nutrient leakage from agriculture, emission of acidic substances from industry and traffic, fish farming, canalisation to avoid floods, and dams to produce electricity etc, and hence contributed to e.g. eutrophication, pollution and acidification. However, some of these influences have undoubtedly been favourable to the cormorants. For example, eutrophication may have lead to changes in composition of fish communities and increased productivity (Persson et. al 1991). High productivity means more fish available to the cormorants and compositional changes means a trend towards larger populations of e.g. perch *Perca fluviatilis*, ruff *Gymnocephalus cernua*, roach *Rutilus rutilus*, bream *Abramis brama* and other cyprinids which are easy to exploit for the cormorants (De Nie 1995, van Eerden & Voslamber 1995). Cormorants do well also because of fish farming, which has increased considerably in Europe and North America (Glahn et. al 2000) in recent decades. In Europe, carp is the principal species, and fishponds are frequently utilised by foraging cormorants which may sometimes cause substantial economic losses to the fishermen (Osieck 1991). Fish at fishponds appear to be particularly vulnerable to cormorant predation during the winter, and cormorants breeding in Sweden presumably benefit by good foraging conditions at fishponds in connection with their migration through Europe. In recent years, increasing concentrations of cormorants have been observed over-wintering in South Swedish waters (Bengtsson 1999). This may be due to saturation in traditional over-wintering areas (Suter 1995a), but possibly also related to improved foraging conditions, and less severe winter climate in northern areas.

The effect of hunting and human disturbance

Probably few other birds in Sweden have in recent years been subjected to more intense persecution than the cormorant. Illegal actions have been frequent and involved destruction of eggs, killing of young and deliberate disturbance at potential breeding sites. For example, during the period 1985–1999, a total of at least 42 colonies (19%) were subjected to occasional or repeated illegal actions (Table 3). Of these colonies, 23 are thought to have vanished due to persecution. In 19 cases illegal actions have involved birds breeding within protected areas. Moreover, the actual amount of illegal actions probably is higher than shown here, since less severe actions probably only rarely are observed. Legal measures to control cormorants have involved shooting of birds at or near standing fishing gears and egg pricking at colonies. Up to now egg pricking is known to be carried out in at least 19 colonies, and reported shooting involved between 895 and 3864 birds per year (1994–2000) (Table 5).

For many years, management actions against cormorants have been most intense in the provinces of Småland and Östergötland. However, with expanding cormorant populations legal and illegal actions have increased, and permits to shoot cormorants in order to protect fishing gears and fish therein, and/or egg pricking are currently issued by 11 of 16 local authorities where cormorants breed. No simple relationship exists between the amount of damage caused by cormorants to the fishery and the measures taken against cormorants (see also Engström 1998).

Modelling the effect of hunting on population size

How would cormorant populations have developed if no hunting or other actions against the cormorants had taken place? Probably the best information currently available comes from population models. These models aim at studying the interaction between hunting and density-dependence in regulating population sizes. Frederiksen et al. (2001) studied the effect of hunting on the whole North-west European cormorant population and modelled different scenarios with varying assumptions about the strength of density dependence in adult survival and proportions breeding. The most well-supported scenario indicates that the effect of hunting at the present level (17,000 cormorants reported shot in 1998/1999) was small (<10% reduction in population size when at equilibrium). In this model the total European population consisted of 500,000 individuals (100,000 pairs). However, when shooting was increased to 65,000 birds per year a critical level was reached and the population started to decrease in size. Converted to the Swedish situation, an estimated 127,000 individuals (25,600 pairs times a correction factor of 4.7–5.2 equals 120,000–133,000 individuals), the critical level (13%) appears at 16,000 – 17,000 birds shot per year. In their model Frederiksen et al. (2001) used values from a stable population, while the actual number needed to be shot to stabilise or to decrease bird numbers in an expanding population (such as in Sweden) would probably be even higher. Data from Sweden indicate that hunting in no year probably have exceeded 4000 shot cormorants (Table 5). Hence, it seems as if the local reductions carried out, in terms of number of shot birds, so far can have had only a marginal effect when the whole Swedish population is taken into account.

Effects on a regional level

What do we know about the effects of hunting and egg pricking on populations on a regional scale? It is obvious that the colonies subjected to human interference in many cases are severely affected. For example, of five known sites where cormorants nested in trees and the trees were felled, the cormorants did not return, or returned only with some few pairs in the following year(s). However, when cormorants nest on ground and eggs are picked, the cormorants seem to be more reluctant to leave their sites (at least so for old colonies) and cormorants sometimes continue to use the sites for several more years. However, when colonies are subjected to repeated disturbance, year after year, numbers are usually much reduced and sites finally abandoned (e.g. the islands of Bockskär and L. Gjusbådan in Östergötland).

What happens to birds that are forced to leave a former breeding site, for example when nesting trees have been cut? In the case of the colony at Gåsö (exterminated when holding ca 3000 pairs), most birds seem to have switched to other neighbouring colonies. This is supported by the fact that the total number of breeding pairs within a radius of 20 km from Gåsö changed only marginally when counts are compared for the years before and following the destruction. In 1992, 2971 pairs bred at four colonies, in 1993 (the year of destruction), 2855 pairs at seven colonies, and in 1994, 2776 pairs at six colonies.

In recent years, large ground-breeding colonies on the islets of Millgrunden, Mannegrund and Södreskär in Northern Kalmar Sound have repeatedly been destroyed (legally) through egg pricking. In 1999, a colony at the nearby island of Pata Eneskär increased considerably in size from 185 pairs in 1998 to about 2100 pairs in 1999. The most probable cause behind this sudden and strong increase is movements of birds from the disturbed colonies. The above example, and experiences also from other colonies, indicate that disturbance or measures to control cormorants locally by egg pricking in general only have had small effects on population size within regions. In some cases, disturbance may even have contributed to accelerated dispersal of colonies (e.g. the colony Gåsö). In the light of present actions, it seems as if the cormorants, when disturbed, most likely will move to another site, as long as there are some protected and/or undisturbed sites available to them. Only when such safe sites are limiting to the birds (or when cormorants are regulated by other means, e.g. by food availability) the number of birds within a region could be expected to level off or decline. At present, cormorants in Sweden appear, in general, not to be limited by the amount of suitable sites for breeding, and when disturbed cormorants can, more or less freely, move to other sites.

Thus hunting and egg pricking seem to have had only small effects on population size. Moreover, when areas with low disturbance (e.g. the coastal areas of Skåne and Blekinge) are compared with areas with extensive disturbance (e.g. the coastal areas of Småland and Östergötland), populations stabilised at about the same time (1995–1996, Table 1), and most likely other factors than hunting and disturbance are responsible for the stabilisation in population numbers.

Conclusion

The spectacular population development of the Great Cormorant in Sweden during the last fifteen years has now partly come to a halt. However, in Lake Mälaren, Lake Hjälmaren and some coastal areas including the provinces of Södermanland and Uppland, cormorant numbers continue to increase at a high rate. The population, which currently covers most of South Sweden (except for a sparse occurrence on the west Coast), and some scattered colonies along the coast of the Bothnian Gulf, is vigorous and no obvious threat appears to exist at the moment. The actions currently carried out to limit population sizes are small in relation to amount of actions needed, according to a population model, to decrease cormorant numbers. Since problems related to cormorants generally are largest during the summer (i.e. damage to fish in fishing gears), I consider present actions to reduce cormorant numbers to be of limited value. This is because cormorants are very mobile at this time of the year and birds that cause damage to fishery only partly comes from local populations.

Finally, it is important to continue to follow the population development in the different regions, to study the effects of control measures (both legal and illegal) on population sizes, and to develop non-lethal methods to reduce cormorant induced damage to fishery.

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Sammanfattning

Förekomsten av storskarv Phalacrocorax carbo *i Sverige med särskilt tonvikt på den sentida populationsökningen*

Som få andra fågelarter har det svenska beståndet av mellanskarv genomgått en anmärkningsvärd populationstillväxt och spridning under senare år. Populationsutvecklingen har varit så kraftfull att beståndet idag, med stor sannolikhet, är större och täcker ett vidare geografiskt områden än någonsin tidigare i historien. Storskarv av rasen *Phalacrocorax c. carbo* har funnits i Östersjöområdet sedan minst 9000 år – och förmodligen även häckat här under större delen av den tiden. När exakt storskarven försvann som häckfågel och ersattes av nuvarande mellanskarven *Ph. c. sinensis* går inte att fastställa. Olaus Magnus (1590) antyder att skarven (mellan-) möjligen häckade i landet, men varken Carl von Linné eller Olof Rudbeck d.y. omnämner häckande skarvar. Arkeologiskt material som indikerar häckande storskarv är som yngst från 900-talet. Från omkring början av 1800-talet finns säkra belägg för häckande mellanskarv i Skåne och Blekinge. De små och geografiskt begränsade populationerna i Skåne och Blekinge utsattes regelmässigt för sabotage. Detta motverkade troligen spridning och mot slutet av 1800-talet, eller möjligen något senare, försvann arten som häckfågel i Sverige. Mänsklig förföljelse berörde bestånden kraftigt även i andra delar av Europa och antalet skarvar förblev under lång tid mycket litet. Mot slutet av 1940-talet började skarven ånyo häcka i Sverige på Svartö i Södra Kalmarsund. Uppdykandet på Svartö sammanfaller väl i tiden med borttvingandet av en koloni på ön Rügen i Tyskland samt expanderande skarvbestånd i Danmark. Fram till och med 1965 utsattes Svartöskarvarna för liten men begränsad jakt. Märkligt nog, även långt efter det att jakten upphörde, förblev tillväxten mycket låg – och rimligen måste även andra faktorer än jakt spelat roll för populationsregleringen.

Så småningom, med stärkt naturvårdssyn, gavs skarven ett ökat skydd i delar av Europa och fridlystes i kärnområdena i Nederländerna (1965) och Danmark (1971). År 1979 gavs skarven ett omfattande skydd genom att arten uppfördes på EU:s så kallade Fågeldirektiv. Det västeuropeiska beståndet bestod då av ca 5000 par Vid sidan om skydd antas förbättrade födoförhållande varit avgörande för skarvbeståndets gynnsamma utveckling. Detta har skett bl.a. genom ett ökat antal fiskodlingar, uppdämningar och kanaliseringar och av floder, samt eutrofiering – faktorer vilka bidragit till rikare och för skarvarna mer lättexploaterade fiskbestånd.

I Sverige var beståndsökningen särskilt kraftfull mellan 1986 och 1994 (31% per år) och antalet par ökade från 1800 till 15.500. Efter 1994 har en uppbromsning skett i kärnområden i Skåne, Blekinge, Småland och Östergötland. Kring mitten av 1990-talet nådde skarven i princip sin nuvarande geografiska utbredning. Under andra halvan av 1990-talet har ökningen fortsatt att vara kraftig i glest besatta och perifera områden, d.v.s. kustområden i Södermanland, Uppland och Gotland samt i flera insjöar. År 1999 hade beståndet stigit till ca 25.600 par fördelade på ca 154 kolonier (inkl. fyra solitärhäckningar). De största kolonierna finns i östra Blekinge (Fröstensskärv 1613 par 2000), i Kalmarsund (Svartö/Törnholmen/N Sandholmen 2303 par, Svartingskär 1900 par och Pata Eneskär 2100, samtliga 1999), och på Gotland (Lilla Karlsö 2268 par 2000). Största genuina sötvattenskolonin finns i Vänern (627 par, Kållandsö, 2000).

Efter att Sverige blev medlem i EU 1995 upphörde den allmänna jakten på skarv. Länsstyrelserna kan dock bevilja undantag från det generella jaktförbudet enligt Artikel 9 i Fågeldirektivet. På grund av ökade populationstätheter och de skador skarven anses orsaka på fisket, och skador i vissa fall på naturmiljön, tillåter ett flertal länsstyrelser (11 av 16 med häckande bestånd av skarv) skyddsjakt idag i någon form. Mest omfattande har jakten hittills varit i kustområden i Småland och Östergötland, men i takt med att bestånden ökat har jakt på skarv kommit att beröra allt fler områden. Exempelvis har omfattande jakt bedrivits i Hjälmaren under 1999 och 2000. Utöver legal jakt är skarven utsatt för omfattande illegal förföljelse främst genom sabotage på skarvarnas häckningsplatser. Till exempel, mellan 1985 och 1999 utsattes inte mindre än 17 kolonier i Kalmar län för störning varav 10 illegalt. I Östergötland var motsvarande siffra 22 varav 17 illegalt. Den mest omtalade störningen ägde rum 1993 på Gåsö i Norra Kalmarsund då några upprörda yrkesfiskare sågade ner samtliga boträd med omkring 3000 häckande par. Hur stor påverkan störningar haft på lokala bestånden är svårbedömt då störningarnas omfattning i många fall inte varit möjliga att kvantifiera. Likaså är kunskapen om täthetsreglerande mekanismer på populationsnivå begränsad. Populationsutvecklingen för de olika områdena antyder dock att påverkan varit förhållandevis liten. I flera fall finns tydliga indikationer på att skarvarna vid störning(ar) flyttat till närliggande kolonier och påbörjat häckning där.

Frederiksen et al. (2001) har använt en populationsmodell för att studera effekterna av jakt på populationsnivå och först vid en avskjutning av omkring 13% nåddes en kritisk gräns och beståndet började minska. Omräknat till det svenska beståndet, omfattande en sommarpopulation av ca 120.000–133.000 individer, krävs en årlig avskjutning av minst ca 16.000–17.000 individer för att långsiktigt minska beståndet. Den rapporterade jakten av skarv i Sverige har inget år överstigit 4000 fåglar och effekterna av nuvarande jakt är troligen små. Då problemen med skarvar generellt är störst under sommaren (skador på fisk i redskap) är min bedömning att åtgärder för att begränsa häckande bestånd (i form av äggprickning och jakt) vanligen är av liten betydelse eftersom de fåglar som orsakar problemen delvis härrör från andra bestånd. Populationsutvecklingen i Sverige under de senaste åren antyder att beståndet som helhet nu är nära mättnad. Omkring en fjärdedel Nordvästeuropas mellanskarvar häckar i Sverige som näst efter Danmark (42.000 par 2000) har flest häckande skarvar i Europa.

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Large gulls as predators of passerine landbirds migrating across the southeastern North Sea

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Abstract

The predation by large gulls on passerines migrating across the southeastern North Sea was studied on the offshore island Helgoland throughout 1999; 15,307 pellets of Herring Gull *Larus argentatus* and Great Black-backed Gull *L. marinus* were examined. The main prey was fish and crustaceans, but during migratory seasons of passerines (March to May, August to November) up to 7% of the pellets contained remnants of passerines (mainly thrushes *Turdus* spp. and Starlings *Sturnus vulgaris*, but few species of <50 g body mass). For half-month periods, the number of pellets containing passerines correlated with the number of passerines stopping over on Helgoland for both size categories of <50 g and >50 g. Pellets containing passerines were mainly found during weather conditions favourable for migration, when many birds were aloft, rather than during adverse conditions. Based on the number of large gulls present, an estimated 5200 passerines might have fallen victim to gulls during the year. Although some passerines may be scavenged rather than captured, gulls must be important potential predators for passerines migrating across the sea.

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Introduction

Strategies of migratory bird flight are often discussed regarding the energy cost of the flight, e.g. distances between stopover sites or migration in relation to weather situations (Alerstam 1990, Piersma & van de Sant 1992, Klaassen & Biebach 2000). Another important factor during migration is predator avoidance which may cause birds to migrate at night or at high altitudes. Migration along coastlines is thought to be risky because many raptors also concentrate along coastlines during their own migration (Ulfstrand et al. 1974, Aborn 1994). Raptors, especially falcons, also hunt migrating passerines at sea, either based from coastal islands (Eleonora’s Falcon *Falco eleonorae*) or occasionally during their own migratory flight (e.g. Merlin *Falco columbarius*) (Walter 1979, own obs.). When crossing stretches of sea, passerines may also fall victim to gulls which are often seen to attack migrants (summarized by Macdonald & Mason 1973, Glutz von Blotzheim & Bauer 1982, and hunting method described by Alerstam 1990), leading to the assumption that this kind of food acquisition is commonly occurring in Great Black-backed Gulls *Larus marinus* and Herring Gulls *L. argentatus* during migration of passerines (Vauk & Prüter 1987). Based on these incidents and on observations of passerines ascending to higher flight altitudes during sea crossings at dawn, gulls are supposed to be the most important passerine predators when crossing seas (Macdonald & Mason 1973, Bourne 1980). In a study addressing which factors influence stopover decisions during the migration across an ecological barrier (German Bight, North Sea), predation was thought to be of considerable importance (Delingat & Dierschke 2000). In this context the extent of passerine predation by gulls during the crossing of this stretch of sea can be assessed by examining a large sample of pellets produced by Herring and Great Black-backed Gulls on the offshore island of Helgoland throuhgout the year.

Methods

The island of Helgoland (1.5 km^2) is situated 43 km off the German Wadden Sea coast (54° 11' N, 07° 55'

Table 1. Monthly average numbers of large gulls counted on Helgoland during spring tides (every 15 days) 1992–1998 and maximum numbers in 1999 (Institut für Vogelforschung unpubl. data). Data in addition to the bi-weekly counts are included also for the Lesser Black-backed Gull.
Månadsvisa medelvärden av antalet större trutar räknade på Helgoland vid springflod (var 15:e dag) åren 1992–1998 samt maximiantal 1999 (Institut für Vogelforschung opubl. Data). Data utöver fjortondagarsräkningarna presenteras även för silltrut.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Herring Gull	1992–1998	963	1137	1017	924	564	510	477	665	902	1173	1525	1499
Gråtrut	(SD)	(779)	(589)	(615)	(412)	(177)	(138)	(117)	(97)	(209)	(605)	(820)	(880)
Larus argentatus	1999	527	1403	896	985	308	330	445	650	599	2203	510	410
Great Black-backed Gull	1992–1998	686	385	142	345	242	520	484	1362	1957	986	970	972
Havstrut	(SD)	(742)	(219)	(110)	(158)	(37)	(282)	(175)	(453)	(443)	(339)	(440)	(649)
Larus marinus	1999	163	214	93	132	109	210	425	582	970	1140	264	262
Lesser Black-backed Gull	1992–1998	1	2	25	90	112	158	421	731	348	66	4	5
Silltrut	(SD)	(2)	(2)	(29)	(53)	(58)	(42)	(297)	(546)	(231)	(74)	(5)	(12)
Larus fuscus	1999	1	6	11	50	40	132	100	360	150	90	3	1

E). About 200 pairs of Herring Gulls breed on Helgoland, and in addition several thousand other large gulls are present on Helgoland during the nonbreeding season (Table 1). Herring and Great Black-backed Gulls, and few Lesser Black-backed Gulls *Larus fuscus* roost on piers of a total length of 7 km. From 22 January to 14 December 1999, a total of 15,307 pellets of large gulls were examined on seven piers visited on average every five days. The smaller pellets of Kittiwakes *Rissa tridactyla* were not considered in this study.

Pellets were classified according to their predominant kind of prey based on the largest proportion of visible remnants (see Table 2). Most pellets consisted of only one kind of prey, and this was especially true when birds had been eaten. When containing remnants of birds, pellets were examined more closely and prey species were determined as precisely as possible by feather coloration, bill and feet. For further calculations, passerines were grouped into small (<50 g body mass) and large birds (>50 g). In the latter group, Starlings were sometimes treated separately because their seasonal pattern with large post-breeding assemblages of juveniles differs much from other passerine migrants.

Results of pellet examination were compared to the sum of resting birds counted or estimated on Helgoland daily, and to those trapped in a standardized program in the trapping garden of the Vogelwarte Helgoland with three funnel traps (see Moritz

Table 2. Diet composition of large *Larus* species on Helgoland according to pellet contents in 1999 (percentages). Each pellet was assigned to only one category according to its predominant prey.
Näringsval hos större trutar Larus *på Helgoland enligt analyser av spybollar under 1999 (procent). Varje spyboll klassades bara till en byteskategori beroende på dominerande inneehåll.*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. pellets *antal spybollar*	119	324	2087	894	558	566	1074	1400	3811	2740	1599	135
Fish *fisk*	41.2	62.7	69.3	19.7	31.7	53.2	47.5	72.0	61.2	22.5	24.5	10.4
Crustaceans *kräftdjur*	7.0	13.9	6.9	44.5	43.0	32.3	37.1	17.9	33.2	55.3	35.9	15.6
Molluscs *blötdjur*	4.0	9.6	10.3	15.7	14.0	6.0	2.7	2.7	1.8	4.3	2.5	1.5
Polychaetes *havsborstmaskar*		1.2		7.2	0.4			0.1	<0.1			
Algae *alger*	1.0		6.7	2.5			2.0	1.1	1.7	0.6	2.8	3.7
Garbage *avfall*		1.5	0.3	0.2	0.7	0.2	0.7	0.6	0.9	4.5	1.9	3.0
Kelp flies *tångflugor*				0.6		0.9	0.1	1.4	0.3	8.3	23.7	42.2
Other *annat*		0.3	0.1	1.9	8.2	1.4	0.7	2.8	0.3	0.3	0.1	1.5
Non-passerines *icke-tättingar*	6.5	10.8	1.5	1.1	0.5	4.9	9.4	1.2	<0.1	0.3	1.6	20.7
Passerines *tättingar*			4.8	6.7	1.4	1.1		0.1	0.6	4.0	7.1	1.5

Table 3. Monthly totals of passerines found in pellets of large gulls on Helgoland in 1999.
Månadvisa totalsummor för tättingar återfunna i spybollar hos större trutar på Helgoland 1999.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
species <50 g													
White Wagtail *Motacilla alba*	0	0	0	0	0	0	0	0	1	0	0	0	1
Meadow Pipit *Anthus pratensis*	0	0	0	0	0	0	0	0	0	1	0	0	1
Dunnock *Prunella modularis*	0	0	2	0	0	0	0	0	0	0	0	0	2
Robin *Erithacus rubecula*	0	0	1	1	0	0	0	0	0	0	0	0	2
Common Redstart *Phoenicurus phoenicurus*	0	0	0	0	1	0	0	0	1	0	0	0	2
Northern Wheatear *Oenanthe oenanthe*	0	0	0	0	1	0	0	0	2	0	0	0	3
Garden Warbler *Sylvia borin*	0	0	0	0	0	1	0	0	1	0	0	0	2
Common Whitethroat *Sylvia communis*	0	0	0	0	0	0	0	1	1	0	0	0	2
Great Tit *Parus major*	0	0	0	0	0	0	0	0	0	1	0	0	1
Chaffinch *Fringilla coelebs*	0	0	2	0	0	0	0	0	0	1	0	0	3
Brambling *Fringilla montifringilla*	0	0	0	0	0	0	0	0	0	0	1	0	1
Greenfinch *Carduelis chloris*	0	0	0	0	0	0	0	0	0	1	0	0	1
Linnet *Carduelis cannabina*	0	0	1	0	0	0	0	0	0	0	0	0	1
Subtotal species <50 g	**0**	**0**	**6**	**1**	**2**	**1**	**0**	**1**	**6**	**4**	**1**	**0**	**22**
species >50 g													
Ring Ouzel *Turdus torquatus*	0	0	0	0	1	0	0	0	0	0	0	0	1
Blackbird *Turdus merula*	0	0	36	12	0	0	0	0	0	15	32	2	97
Fieldfare *Turdus pilaris*	0	0	0	0	1	0	0	0	0	0	1	0	2
Redwing *Turdus iliacus*	0	0	5	6	0	0	0	0	0	32	6	0	49
Song Thrush *Turdus philomelos*	0	0	11	5	0	0	0	0	3	12	3	0	34
Redwing/Song Thrush *T. iliacus/philomelos*	0	0	3	2	0	0	0	0	1	3	1	0	10
Starling *Sturnus vulgaris*	0	0	20	9	0	3	0	0	0	29	62	0	123
Subtotal species >50 g	**0**	**0**	**75**	**34**	**2**	**3**	**0**	**0**	**4**	**91**	**105**	**2**	**316**
Unidentified passerines	0	0	18	25	4	2	0	1	11	14	7	0	82
Total	**0**	**0**	**99**	**60**	**8**	**6**	**0**	**2**	**21**	**109**	**113**	**2**	**420**

1982 for methods). To evaluate the effect of weather on gull predation on passerines, the weather factors wind force, cloud cover and visibility were compared between the overall migration period of large passerines (1 March to 30 April and 20 September to 30 November, respectively) and the occurrence of large passerines in gull pellets (pooled data of the weather present at the finding of each pellet). The difference in the distribution to the categories of weather data between the day of the migratory period and the birds found in pellets was tested by χ^2-tests and omitting null categories. The exact date of

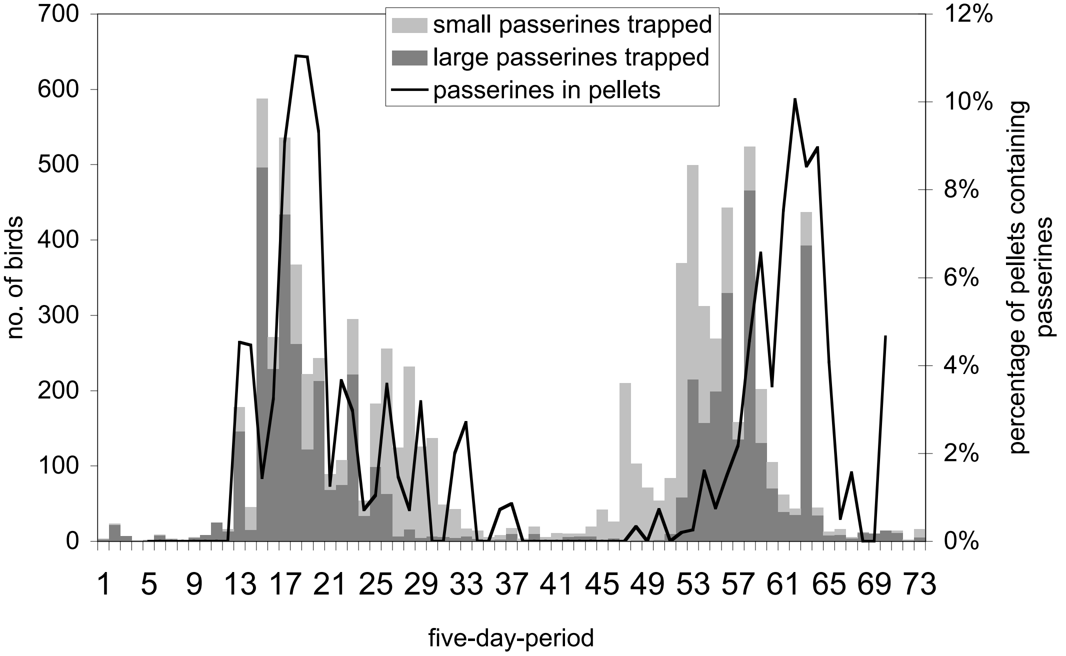

Figure 1. Totals of large and small passerines caught in the trapping garden and the percentage of pellets containing remnants of passerines per five-day-period.
Totalantal stora och små tättingar fångade i fångstträdgården på Helgoland och procentuella andelen spybollar från trutar som innehåller rester av tättingar per femdagarsperiod.

pellet production was unknown, therefore average weather conditions for the preceeding two and three days (including the day of finding) were used for calculations.

Results

According to the pellets, the diet of large gulls varies by season (Table 2). Main prey were fish and crustaceans, but kelp fly larvae found in wrack beds of the island were of considerable importance during storms from October to December (Table 2). In winter months with stormy weather, remnants of seabirds were found in a large proportion of pellets. Non-passerine birds eaten by gulls in late spring and summer (Table 2) were exclusively chicks of Kittiwakes and Guillemots *Uria aalge*. Both species breed numerously on the cliffs of the island (Hüppop 1997).

During the study, 420 out of 15,307 (2.7 %) gull pellets found contained remnants of passerine birds. A total of 19 species could be identified, but the number of prey species involved was probably higher because the identity of prey was unknown in 82 pellets. Three species of thrushes and the Starling were most often found in pellets, while small species (<50 g) occurred only occasionally (Table 3). Although small passerines made up 69.5 % of the total of 58,336 passerines (excluding Starling and corvids) counted or estimated during stopovers on Helgoland from August to November on a daily basis, only 10.1 % of remnants belonged to this size class in gull pellets. In addition, some non-passerine birds classified as migrants rather than seabirds were preyed upon (two Water Rails *Rallus aquaticus*, five Moorhen *Gallinula chloropus*, one Redshank *Tringa totanus*, one Common Snipe *Gallinago gallinago* and two Great Spotted *Woodpeckers Dendrocopos major*).

Passerines were found in pellets only during their migratory seasons (Table 2 and 3), mostly in March/April and October/November, coinciding with the passage of large passerines (body mass >50 g; Figure 1). In both small and large passerines (excluding Starling), the number of pellets found per half month period (August to November; n = 8) correlates with the number of resting birds counted on the island (small passerines: R_S = 0.852, P = 0.007; large

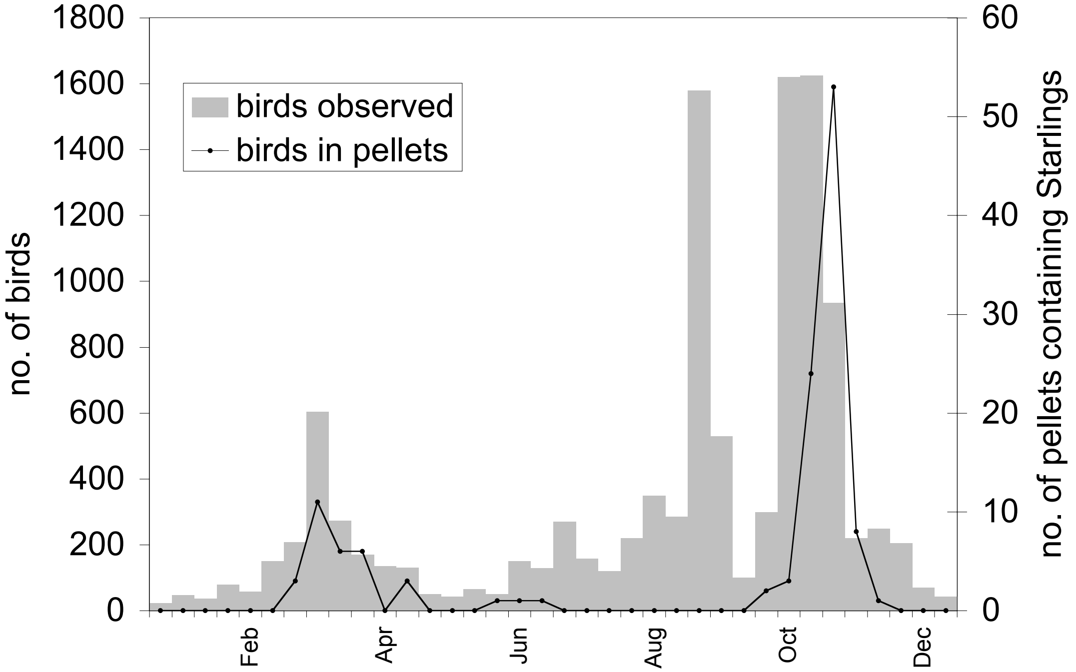

Figure 2. Maximum numbers of Starling observed on Helgoland per ten-day-period in 1999 and the respective number of pellets containing remnants of Starlings.
Maxantal observerade starar på Helgoland per tiodagrsperiod under 1999 samt respektive antal spybollar innehållande rester av stare.

passerines: $R_S = 0.927$, $P = 0.007$). The number of pellets containing Starlings coincide with the seasonal pattern of occurrence of this species (Figure 2). However, no correlation between bird occurrence and birds found in pellets was evident on a finer scale, e.g. between the percentage of Blackbirds or Redwing/Song Thrush in the diet of gulls and the number of birds of the respective species trapped at the bird observatory (Table 4). There is no explanation for the exceptionally high number of pellets (37) containing Starlings on 3 November. There was no large-scale passage or unusual weather recorded those days. In general, there was no indication that passerines were more often captured by gulls during weather conditions adverse to migration. When compared to the overall occurrence of weather conditions during thrush and Starling migration (1 March to 30 April and 20 September to 30 November), pellets containing large passerines were found in periods with less wind and clearer skies, and with good visibility in most cases (Figure 3, Table 5).

Discussion

The contents of the large sample of pellets collected on Helgoland in 1999 reflect the large spectrum of prey taken by Herring and Great Black-backed Gulls (Glutz von Blotzheim & Bauer 1982). A high degree of opportunism in food selection was apparent. Prey available only for brief periods was found in high percentages in pellets temporarily, such as polychaetes during swarming (April), seabird chicks during rearing (June to July) and kelp fly larvae during mass occurrence (October to November). The same holds true for passerine birds, which were found exclusively during passerine migratory periods. Passerine predation by gulls thus seems to be opportunistic because it occurs during periods of high availability.

The many incidents observed of migrating passerines captured by large gulls at sea (Macdonald & Mason 1973, Glutz von Blotzheim & Bauer 1982), also around the island of Helgoland (own obs.), suggest that the passerines found in gull pellets on Helgoland were predated by the gulls. As there is no information about the body condition of the passer-

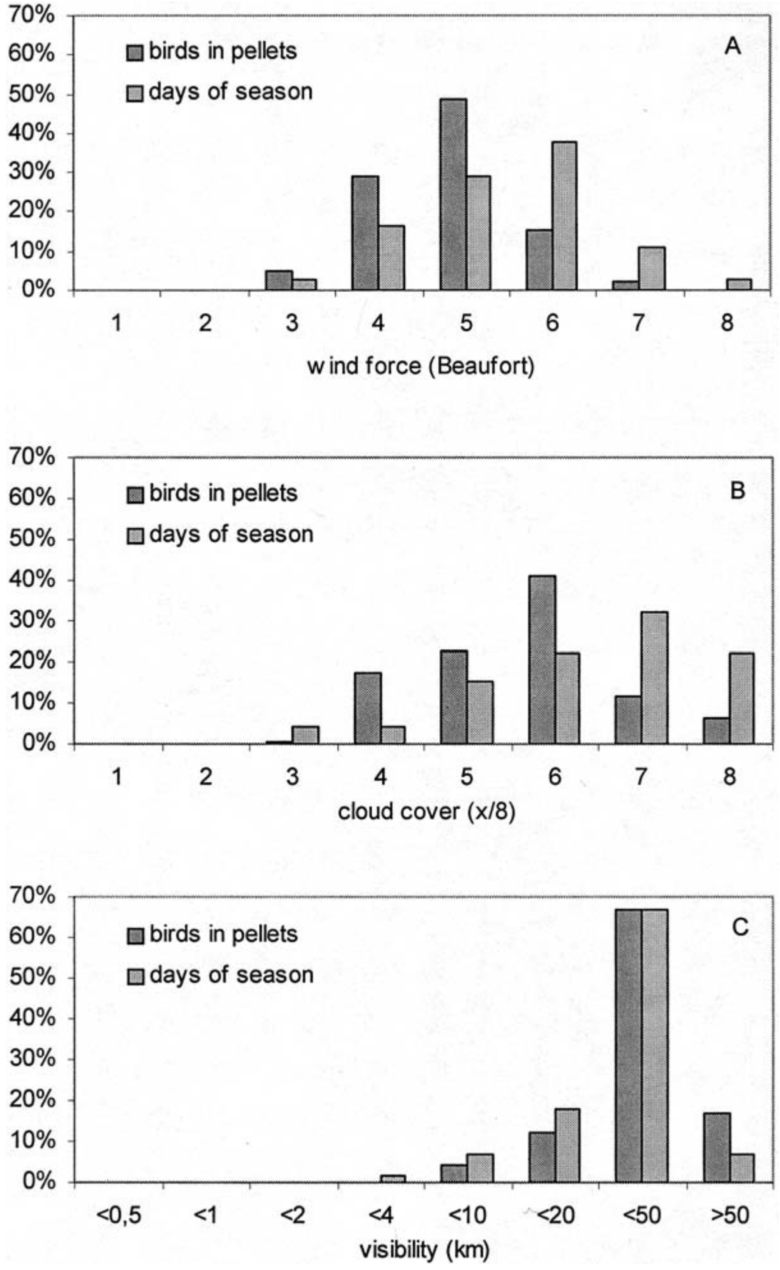

Figure 3. Weather conditions occuring on days in the autumn migratory period of Starlings and thrushes (20 September – 30 November, n = 72; expressed as the average of day of finding and the preceeding day) and at each finding of a pellet containing remnants of Starling or thrushes (average values for two days; n = 199). A: wind force, B: cloud cover and C: visibility. For statistics see Table 5. Nearly the same results were found when using three-day-periods and during spring migration (not shown, but see Table 5).

Väderförhållanden under perioden för starars och trastars flyttning under hösten (20 september–30 november, n= 72; beräknat för dag då spyboll hittades och dagen före) samt väderförhållandet vid påträffandet av spybollar innehållande rester av stare eller trastar (medelvärden för två dagar; n= 199). A: vindstyrka, B: molntäcke, C: sikt. Statistik presenteras i Tabell 5. I stort sett identiskt resultat erhölls då analysen baserades på tre dagars medelvärden samt under vårflyttningen.

Table 4. Spearman rank correlations between percentage of pellets containing remnants of Blackbirds and Redwing/Song Thrush, respectively, and the number of trapped birds of the respective species at the Helgoland bird observatory on either the same day or the same and preceeding day of pellet collection. Days with less than 40 pellets were omitted from the analyses.
Spearman rankkorrelationer mellan procentuell andel spybollar innehållande koltrast eller rödvinge-/taltrast och antalet fångade fåglar av respektive art vid Helgolands fågelstation samma dag eller dagen före spybollen insamlades. Dagar med färre än 40 spybollar uteslöts.

Species *Art*	Season *säsong*		Same day *samma dag*		Same + preceeding day *samma + följande dag*	
		n	R_S	P	R_S	P
Blackbird *Koltrast*	spring (4 Mar – 4 Apr)	17	-0,319	0,211	-0,075	0,774
	autumn (6 Oct – 26 Nov)	30	-0,070	0,711	-0,038	0,842
Redwing and Songthrush	spring (4 Mar – 9 May)	23	-0,056	0,799	0,196	0,371
Rödvinge och taltrast	autumn (13 Sep – 14 Nov)	37	0,179	0,288	0,122	0,470

ines taken, it is impossible to judge whether especially weak birds are selected by hunting gulls. The usual method of capture by forcing a passerine onto the sea surface (Alerstam 1990) may indicate that birds in good condition could be able to escape such attacks by flying upwards (own obs., see also Hedenström & Rosén 2001). It is possible that many or even most passerines were exhausted and alighted on the water before taken by gulls, and finally, it cannot be excluded that gulls scavenged on passerines which were already dead. However, despite being in the digestive tract of a gull for a while, the feathers found in the pellets looked rather intact and differed from feathers of birds washed ashore. Therefore, it is unlikely that the gap between peak migration of passerines and the peak of birds in pellets (Figure 1) is due to dead birds taken after weeks of drifting in the sea.

The high proportion of passerines in the diet of large gulls has not been described before. On Helgoland, few or no passerines at all were found in stomachs or pellets in most earlier studies (Table 6), compared to up to 7 % of pellets containing passerines in April and November 1999. These two months

Table 5. Bonferroni corrected significance levels of differences in distributions of weather conditions during the period of thrush and Starling migration and at the finding of large passerines in pellets. Average conditions for two- and three-day-periods (including the day of finding) were calculated. Sample sizes are 61 days and 111 birds in pellets in spring and 72 days and 199 birds in pellets in autumn.
Bonferronikorrigerade av signifikansnivåer för skillnaderna mellan väderbetingelser under trast- och starflyttningsperioden och förekomsten stora tättingar i funna spybollar. Genomsnittliga förhållanden för två- och tredagarsperioder (inklusive dagen då spybollen hittades) beräknades. Stickprovsstorlek var 61 dagar och 111 fåglar i spybollar för våren och 72 dagar och 199 fåglar i spybollar för hösten.

	two days			three days		
	χ^2	df	P	χ^2	df	P
Spring migration *Vårflyttning* (1 Mar – 30 Apr)						
Wind force *vindsstyra*	20.06	4	<0.01	17.37	3	<0.01
Cloud cover *molnighet*	5.04	6	n.s.	13.65	6	n.s.
Visibility *sikt*	11.92	4	n.s.	7.03	4	n.s.
Autumn migration *Höstflyttning* (20 Sep – 30 Nov)						
Wind force *vindstyrka*	35.53	4	<0.01	9.11	4	n.s.
Cloud cover *molnighet*	35.00	4	<0.01	13.55	4	<0.05
Visibility *sikt*	7.07	3	n.s.	7.74	3	n.s.

Table 6. Proportions of passerine birds in the diet of large gulls on Helgoland. Pellets collected from May to September may in part originate from Lesser Black-backed Gulls.
Proportionen tättingar i dieten hos större trutar på Helgoland. Spybollar som samlades in från maj till september kan delvis härröra från silltrut.

Species and method *Art och metod*	n	Season *Säsong*	No. passerines *Antal tättingar*	% passerines *% tättingar*	Source *Källa*
Herring Gull *Gråtrut*					
Stomachs *magar*	198	Jan–Dec	7	3.5 %	Löhmer & Vauk 1970
Stomachs *magar*	351	Oct–Apr	4	1.1 %	Prüter 1986
Pellets *spybollar*	148	Jun–Jul	0	0.0 %	A.-K. Dierschke in prep.
Great Black-backed Gull *Havstrut*					
Stomachs *magar*	54	Aug–Apr	1	1.8 %	Kock 1974
Stomachs *magar*	134	Oct–Apr	1	1.1 %	Prüter 1986
large gulls *trutar*					
Pellets *spybollar*	784	Aug–Sep	0	0.0 %	Löhmer & Vauk 1969
Pellets *spybollar*	126	Mar	15	11.9 %	Geiß 1994
Pellets *spybollar*	167	Apr	3	1.8 %	Geiß 1994
Pellets *spybollar*	130	May	3	2.3 %	Geiß 1994
Pellets *spybollar*	15307	Jan–Dec	420	2.7 %	this study (details Table 2)
Pellets *spybollar*	176	Dec–Jan	0	0.0 %	Wurm & Hüppop in prep.
Pellets *spybollar*	57	Feb	1	1.8 %	Wurm & Hüppop in prep.

were characterized by very low numbers of large gulls present compared to the average of the years before (Table 1). Because the size of gull roosts on Helgoland is closely connected to the activity of fishing vessels around the island (Hüppop & Wurm 2000) and because discards are an important food of large gulls at Helgoland (Löhmer & Vauk 1970, Kock 1974, Garthe 1993), the low activity of human fisheries during this study (own obs.) is possibly a reason for the high proportion of passerines in the diet of gulls in April and November. An even higher proportion of passerines was found only in a small sample of pellets in March 1993 (11.9 %, Table 6), also in a period of low human fisheries activity (O. Hüppop pers. comm.).

Consistent with an earlier review of passerine predation by gulls (Macdonald & Mason 1973), the majority of passerines taken by large gulls were thrushes and Starlings. Despite their higher abundance smaller passerines were found in pellets only occasionally. One might argue that the later migration in spring and the earlier passage in autumn of small passerines (Figure 1) less often brings these species into adverse weather conditions which was supposed to be advantageous for gulls when hunting migrating passerines (Macdonald & Mason 1973). The results of the present study do not confirm a higher occurrence of passerines in pellets during bad weather. In contrast, more pellets containing passerines were found during periods of good conditions for migration when many passerines were on the wing and therefore available for gulls. It is possible that smaller passerines are better in manoeuvrability compared to larger species (see Hedenström & Rosén 2001), making catching more difficult for gulls. It seems more reasonable that small birds are not a profitable prey for large gull species.

Because only part of the gull roosts on Helgoland are accessible, and the number of pellets produced by a gull during a given period is unknown, it is difficult to estimate the total number of passerines taken by large gulls. Assuming that a pellet is produced every two days, and that maximum values of the bi-weekly gull counts are representative for the whole month, the percentages of passerines found in pellets result in c. 2000 passerines captured during spring migration (March to June) and c. 3200 passerines from August to December. Compared to the number of 420 passerines actually found, the estimate of c. 5200 passerines captured seems reasonable. Unfortunately, the total number of passerines migrating over the German Bight and the number of birds killed by other causes during migration are difficult to estimate. But the birds taken by gulls compare to the number of birds trapped in the trapping garden (in 1999: 8557 passerines year round) or found as victims of feral cats (in 1999 at least 308 passerines). Furthermore, 782 Sparrowhawks *Accipiter nisus* and 119 Merlins *Falco columbarius* were observed on Helgoland in 1999. Most Sparrowhawks and Merlins pass the island quickly, therefore the number of passerines taken by them is probably lower compared to predation by gulls. In the light of these considerations large gulls appear to be significant predators for migrating passerines. Therefore, it makes sense for passerines to adapt migratory strategies to this danger by avoiding flights close to the sea surface during daylight (Bourne 1980).

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Sammanfattning

Trutar som predatorer på flyttfåglar i sydöstra Nordsjön

Flyttfåglar utsätts för många faror under flyttningen. Predatorer kan specialicera sig på förbiflyttande fåglar som t ex hos eleonorafalken *Falco eleonorae*, medan vissa fågelpredatorer själva är flyttfåglar och således jagar under flyttningsresan. På Helgoland förekommer stora mängder gråtrut *Larus argentatus* och havstrut *L. marinus*, vilka huvudsakligen livnär sig på restavfall från fisket som förekommer runt ön. I den här studien samlades 15307 spybollar in från de två trutarterna under 1999 och analyserades med avseende på innehåll (Tabell 1). Det visade sig att under vår och höst, då stora mängder flyttande tättingar passerar Helgoland, innehöll likaså trutarnas spybollar rester av fåglar (Figur 1). Trutarnas huvudsakliga föda var fisk och kräftdjur, men under

flyttningsperioderna (mars–maj, augusti–september) innehöll upp till 7% av spybollarna rester av fåglar (Tabell 2). Materialet delades upp i två storlekskategorier bestående av mindre tättingar (<50 g) och större arter som trastar och stare (>50 g). Artbestämda byten redovisas i Tabell 3. Förekomst av stare i spybollar sammanföll tydligt med starens förekomst på Helgoland (Figur 2), medan ingen signifikant korrelation förelåg mellan procentuell andel av koltrast och rödvinge/taltrast i spybollarna i relation till fångstsiffror vid fågelstationen på ön (Tabell 4). Analys av förekomst av fågelrester i spybollarna i relation till olika väderfaktorer visade en signifikant inverkan av vindstyrka (vår och höst) och molntäcke (endast höst), medan sikt ej verkade förklara variationen av fåglar som trutbyten.

De större arterna (trastar och stare) var betydligt vanligare som byten än de mindre tättingarna (Tabell 3), vilket kan bero på den relativa manövreringsförmågan mellan trutarna och bytesarterna (trastar har sämre manövreringsförmåga än små tättingar) eller att trutarna selektivt jagar större byten p g a bytets profitabilitet (= näringsutbyte i relation till kostnaden att fånga det). Slutligen jämförs proportionen tättingar återfunna i spybollar hos trutar med andra studier (Tabell 6). Det kan inte uteslutas att fågelresterna som återfanns i spybollarna har konsumerats som kadavaer snarare än att trutarna verkligen fångat levande fåglar (såsom antas i denna uppsats). Flera observationer av lyckade jakter på levande fåglar av trutar har emellertid gjorts, vilket stödjer antagandet att trutar faktiskt jagar fåglar opportunistiskt under flyttningen.

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Biometrics of Turnstone *Arenaria interpres* migrating in autumn through the Gulf of Gdańsk region

WŁODZIMIERZ MEISSNER & LESZEK KOZIRÓG

Abstract

In this study we analyse biometrical data of 69 adult and 389 juvenile Turnstones *Arenaria interpres* caught during autumn migration when passing through the Gulf of Gdańsk in the period 1983–1999. Adults had significantly longer wings than juveniles. Mean values of other measurements did not differ significantly between the age classes. Adults migrating early were larger than those passing the study area later. These earlier and larger migrants are regarded as females, which leave nesting areas before the somewhat smaller males. Data obtained from 67 juvenile Turnstones caught at least twice in the same season showed that juvenile Turnstones may have more than one migration strategy when departing from the Gulf of Gdańsk. Some of them behave as energy minimising migrants and migrate with low fat reserves in small steps. The others stay longer, build up large energy reserves (up to 50% of their initial body mass) and are probably able to reach West Africa in one flight.

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Introduction

The Turnstone *Arenaria interpres* is a regular migrant along the southern Baltic coast. This species migrates in small flocks and the annual number of ringed birds and the ringing recovery rate are low (Brenning 1986, Gromadzka 1998, Meissner & Remisiewicz 1998, Stolt et al. 2000). Moreover, data on biometrics and body mass changes at Baltic stopover sites have not yet been published. An analysis of ringing recoveries showed that the majority of Turnstones passing through the southern Baltic originates from Fennoscandia (Meissner & Koziróg 2000). Negligible ringing activity in northern Russia makes presumptions about the eastern range of birds appearing in the Baltic area very speculative. It has recently been stated that the borders between breeding and wintering areas of different populations are not so clear as had been suggested (Underhill et al. 1999, Meissner &Koziróg 2000). Birds that stop in the Gulf of Gdańsk depart in two directions. Probably the majority of them follow the southern Baltic and North Sea coasts, but some of them head directly south to the Mediterranean (Meissner & Koziróg 2000). Low number of Turnstones at inland stopover sites (Harengerd et al. 1973, Tomiałojć 1990) suggests that these birds cover that distance in one flight.

The main aims of this study are to describe the biometrics and migration strategies of Turnstones migrating through the Gulf of Gdańsk and to asses the ability of birds to reach wintering sites in one flight.

Material and methods

Birds were caught between 1983 and 1999 in walk-in traps (Meissner 1998a) placed at three sites: at Jastarnia (54º42’N, 18º40’E), in the Reda river mouth (54º39’N, 18º30’E) and at Rewa (54º38’N, 18º31’E) (Meissner & Remisiewicz 1998). Every year the fieldwork started in mid-July and finished in the end of September. This period covered almost the whole Turnstone migration period (Meissner & Koziróg 2000).

Each caught bird was aged following Prater et al. (1977). Measurements were taken as described by different authors; wing length (Evans 1986), total head length (Green 1980), bill length (Prater et al. 1977), tarsus length (Svensson 1992) and tarsus plus toe length (Piersma 1984). Before 1991, total head length and bill length were measured to the nearest 1 mm with stopped ruler, later on with callipers to the nearest 0.1 mm. To combine less and more precise measurements, the latter were rounded to the nearest 1 mm. Birds were also weighed to the nearest 1 g. Every year the accuracy and the repeatability of measurements taken by different ringers were checked as described by Busse (1984). In total, 69 adults and 389 juveniles were measured between 1983 and 1998. Body mass data from 67 juvenile Turnstones caught at least twice in the same season (retraps) were used to calculate body mass changes during the birds' stay. The mean accumulation rate of energetic reserves was calculated for the third day after the first capture, when the increase of body mass became more prominent and the sample size was still sufficient. The same approach was applied in a previous study on Dunlin (Meissner 1998b). For assessing the theoretical flight range of birds, the equation derived by Pennycuick (1975) was used. This formula is quite robust, because it does not take into account the fact that waders often migrate in flight formations, which leads to decrease of flight costs (Hummel 1983). Moreover, improved body-drag coefficient recommended by Pennycuick et al. (1996) results in increasing the distance that a bird can fly with a given fuel mass. Thus, the obtained results should be treated as a minimum possible distance, which could be covered with given fat reserves in still air conditions. Such calculations require assumptions regarding the body mass at the beginning and at the end of the flight. For this analysis, the final body mass of 82g (the mean body mass of 25% of the lightest Turnstones at the first capture) was presumed. Statistical methods followed Zar (1996).

Results

Biometrics

Almost all measurements of juveniles are unimodal. Only in the case of wing length two distinct peaks appeared (Figure 1). Adults had significantly longer wings than juveniles (Table 1, t-test, df=437, t=2.4, p=0.02). Mean values of other measurements did not differ significantly between the age classes (t-test, p>0.05). Adults migrating before 24 July had significantly longer wings (158.2 mm, SD=2.6) than those passing the Gulf of Gdańsk after 9 August (154.5 mm, SD=3.3) (t-test, df=24, t= 3.01, p=0.006). Other measurements did not differ between these two groups of adults (t-test, p>0.05). The number of measured adults was insufficient for more detailed analysis. Juveniles migrating in subsequent decades did not differ significantly in average wing length (ANOVA $F_{5,373}$=1.44, p=0.20), nor in total head length (ANOVA $F_{5,372}$=2.00, p=0.08), bill length (ANOVA $F_{5,367}$=1.60, p=0.16), tarsus plus toe length (ANOVA $F_{4,139}$=2.19, p=0.07) and tarsus length (ANOVA $F_{5,193}$=1.08, p=0.37). Mean body mass of juveniles and adults was similar (Table 1). Juveniles caught later in the season were heavier than earlier migrants (Kruskal-Wallis test, $H_{5,536}$=86.2, p<0,001) (Figure 2). Significant differences occurred between birds caught in September decades and those caught in August decades (Dunn post-hoc nonparametric test, p<0.05). There were no significant differences in body mass among birds caught in different August decades and among birds caught in different September decades.

Body mass changes and theoretical flight ranges

Among adults, only two birds (2.8%) were caught more than once, while in juveniles 67 birds (16.6%) were retrapped. The median length of stay as estimated by recapture intervals of juveniles was 3.9 days. Their body mass showed a significant increase during the stay (r=0.81, t=13.2, p<0.001), although during the first two days after the first capture some birds lost mass (Figure 3). Thus, the mean body mass change rate was significantly lower during the first day of stay (0.4 %/day) (ANOVA $F_{6,76}$=6.33, p<0.0001 – Tukey test). Later, between the second and the seventh day it varied insignificantly between 3.5% and 4.6% per day (Tukey test, p>0.05). In this period juveniles gained on average 3.9 g/day (SD ±2.1g). Some juveniles staying more than one week, build up more than 50% of their initial body mass (Figure 3). The rate of accumulation of reserves calculated for the third day of stay was 3.9%.

Theoretical flight ranges of Turnstones with a body mass between 130g and 162g (10% of the heaviest birds) ranged between 2500 and 3800 km. However, the theoretical flight range of birds which weighed 99g (the average body mass of juveniles) and 88g (the upper limit of 25% of the lightest birds) would be no more than 1200 and 480 km, respectively.

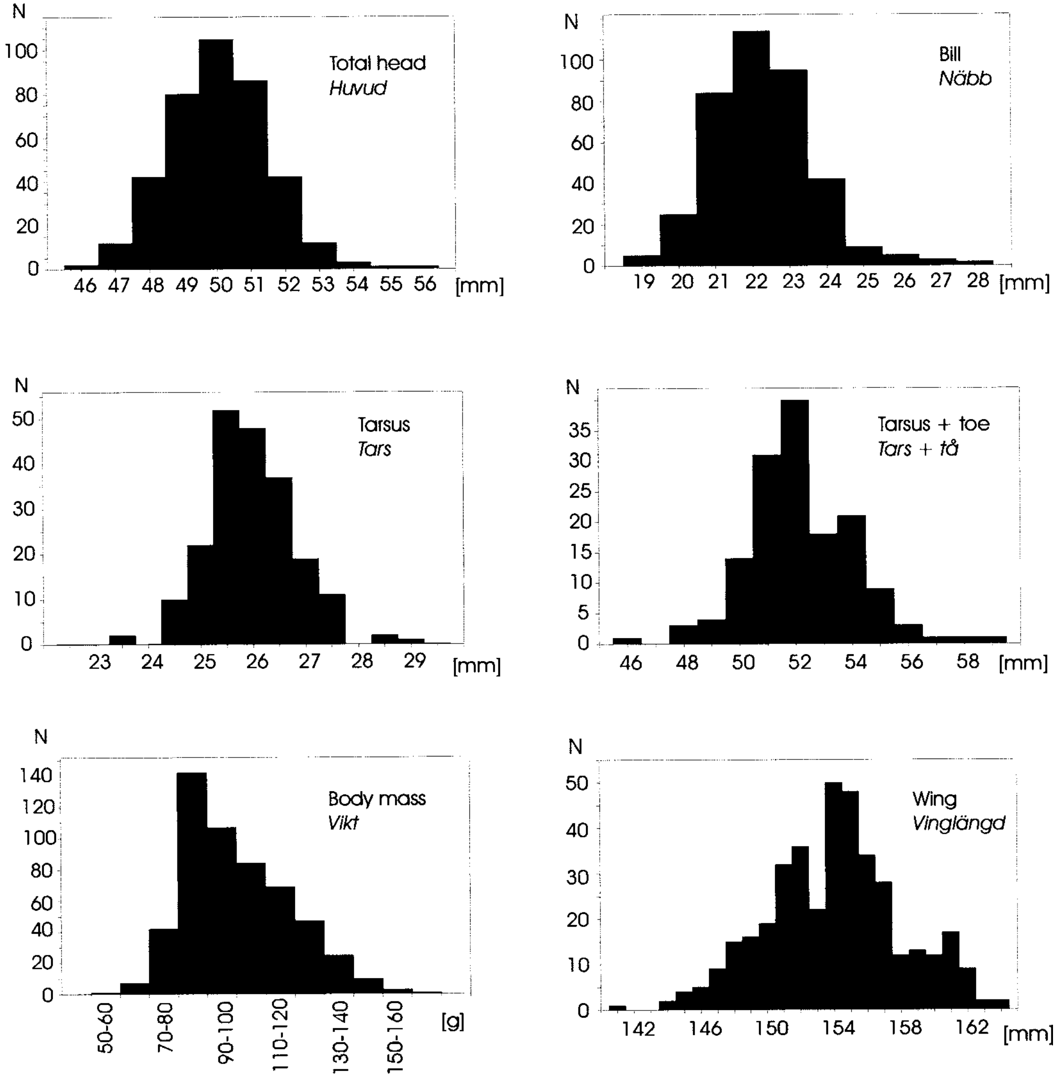

Figure 1. Frequency distribution of different measurements in juvenile Turnstones caught on the coast of the Gulf of Gdańsk in the autumns of 1983–1999
Fördelningen hos olika mått insamlade från juvenila roskarlar fångade i Gdanskbukten under höstarna 1983–1999.

Discussion

Biometrics

The wing length is the best measurement reflecting the sexual dimorphism in Turnstones. Adults migrating early were larger than those passing the study area in the later part. This indicates that females, which have longer wings, leave breeding grounds some days before males. In southern Finland the departure of females starts in mid-July (Glutz von Blotzheim et al. 1975, Liedel & Bianki 1985), which corresponds to the time of arrival of first adults in the Gulf of Gdańsk region (Meissner and Kozirόg 2000). The 3.7 mm-difference in the mean wing length between the earlier and the later migrants is only a little smaller than that reported for males and females after completing moult of primaries in South Africa (Summers et al. 1989).

Turnstones migrating along the southern Baltic

Table 1. Comparison of mean values of measurements between adult and juvenile Turnstones caught at the coast of the Gulf of Gda_sk in the autumns of 1983–1999. Results of statistical tests are given in the text.
Fördelningen hos olika mått insamlade från adulta och juvenila roskarlar fångade i Gdanskbukten under höstarna 1983–1999.

Measurement *Mått*	Adults *Adulta*				Juveniles *Juvenila*			
	Mean	SD	Range *Vidd*	N	Mean	SD	Range *Vidd*	N
Total head (mm) *Huvud och näbb*	50.2	1.8	47–54	64	50.0	1.5	46–56	381
Bill (mm) *Näbblängd*	22.4	1.5	20–25	69	22.4	1.7	19–32	385
Wing (mm) *Vinglängd*	155.4	3.7	146–161	57	154.0	4.1	145–164	382
Tarsus + toe (mm) *Tars + tå*	51.7	1.7	48–55	28	52.2	1.9	46–58	145
Tarsus (mm) *Tars*	25.64	0.8	24.4–27.3	29	25.77	0.8	23.2–30.6	200
Body mass (g) *Vikt*	98.9	13.1	62–136	58	99.0	17.7	55–160	389

coast belong mainly to the Fennoscandian – West Russian population, which winters in the vast area extending from western Europe to western Africa (Summers et al. 1989, Meissner & Kozirόg 2000). Adults start moulting primaries after completion of autumn migration (Pienkowski et al. 1976, Summers et al. 1989). In fresh plumage in western Africa, the mean wing length of adults ranged between 156.9 mm and 157.3 mm (Ens et al. 1990, Wymenga et al. 1990). Birds caught in the Gulf of Gdańsk in autumn had worn primaries and this resulted probably in the lower mean wing length found. Even though adults had worn primaries, the mean wing length of juveniles, which migrate in fresh plumage, was significantly shorter. The same results were obtained in autumn in Scotland, southern Africa (Summers et al. 1989) and also in Australia (Houston & Barter 1990). It seems that the relatively short wing in juveniles may be a general rule in this species, similarly as in Knot *Calidris c. canutus* (Fournier & Spitz 1970, Gromadzka 1992, Meissner 1992) and Grey Plover *Pluvialis squatarola* (Gromadzka & Serra 1998). During autumn migration, adult birds of many other wader species have shorter wings than juveniles, due to the wear of the outermost primary (OAG Münster 1990, Meissner 1997a, b, 1998b).

The published data on biometrics of Turnstones caught within the flyway and wintering range of Fennoscandian – West Russian population are inconsistent. The mean wing length of adults obtained during this study (155.4 mm) is shorter than that reported by Branson et al. (1979) for non-moulting birds staging in the Wash in August (156.7 mm). It is noteworthy that the method used to measure wing was declared as the "maximum chord method" in both studies. Probably the sample from the Wash consisted not only of Fennoscandian – West Russian birds, which usually do not moult there, but also of Nearctic birds which had not started their primary moult after arrival. Turnstones from Greenland and Northeast Canada have longer wings than Fennoscandian – West Russian birds (data from Branson et al. 1979, Summers et al. 1989, Wymenga et al. 1990) and their presence in the Wash sample might have increased the average of the wing length. Average bill lengths in the study and in southern Africa (Summers et al. 1989) are very similar, but they are lower than those measured in Mauritania and Guinea-Bissau (Ens et al. 1990, Wymenga et al. 1990). The majority of Turnstones wintering in West Africa and migrating along the Baltic coasts belong to the same population. Hence it is difficult to explain why birds from Mauritania measured in spring had longer bills than birds migrating in autumn with worn feathers on the forehead. The same difference was found in the case of total head length and tarsus plus toe length (Ens et al. 1990). It is also possible that the manner of taking measurements differed slightly among sites, although it was claimed to be the same.

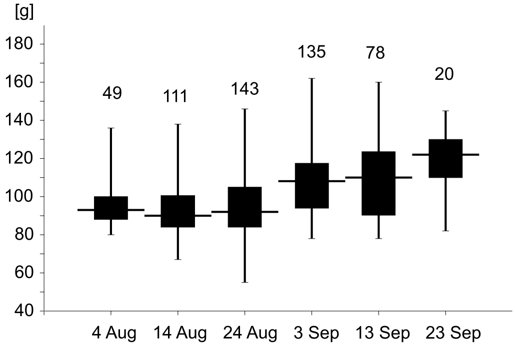

Figure 2. Comparison of body mass of juvenile Turnstones caught in subsequent decades. Horizontal line – median, rectangle – 5% and 95% of the distribution, vertical line – range. Numbers above the bars indicate sample size.
Kroppsvikt hos juvenila roskarlar fångade under olika tiodagarsperioder. De vågräta linjerna anger medianvärde, rektanglarna visar mellan 5% och 95% av fördelningen och de lodräta linjerna variationsvidden. Siffrorna ovanför anger antalet fåglar som vägts i de olika perioderna.

Migration strategy

The low proportion of retrapped individuals in this study means that the majority of Turnstones did not stay in the Gulf of Gdańsk longer than one day. Much lower proportion of retrapped adults might be the result of combination of greater experience (avoidance of traps) and shorter length of stay (lower probability of being recaptured).

The small increment or even the decrease in body mass during the first day of stay is a commonly seen phenomenon, which takes place soon after arrival of the migrating bird at a new stopover site (Mascher 1966, Meissner 1998b). This is probably the main reason for the small increase of body mass in retraps the day after the first capture found in this study and also in other wader species (e.g. Page & Middleton 1972, Meissner 1992, 1998b, Meissner & Górecki in press). Such transitional body mass decrease does not occur later after next recaptures of the same bird at the same stopover site (Meissner 1998b). Thus, it seems to be unlikely that only the stress is responsible for this phenomenon. Moreover, individuals with very low body mass at the first capture do not show body mass decrease (Masher 1966, Meissner 1998b). It is possible that the fattest birds need some time after landing to convert the metabolism of lipids from lipolysis, which takes place during flight, to lipogenesis at the stopover place. In mammals, for instance, it takes from several to over ten hours until the organism is able to start an effective accumulation of fat deposit (Iritani et al. 2000). The increase of body mass in lean individuals, which takes place just after arrival at the foraging site, can result from the increase of water amount in organism in the effect of synthesis and storage of glycogen (Jenni & Jenni-Eiermann 1998, Meissner 2001), which is used as the source of energy for all kinds of activity in the stopover site (Rothe et al. 1987). Ens et al. 1990 reported that in Mauritania Turstones suffered badly from being caught and it took them about 25 days to recover from traumatic effect of catching. All birds trapped in the Gulf of Gdańsk were released after 0.5–3 hours, whereas in Mauritania within 12 hours. The body mass decrease within first few hours in captivity was mainly due to dehydration, whereas fat and lean dry mass loss become prominent after about 4 hours (Davidson 1984). A prolonged time of being in captivity in high ambient temperatures might be the reason for that it took birds in Mauritania a longer period to recovery.

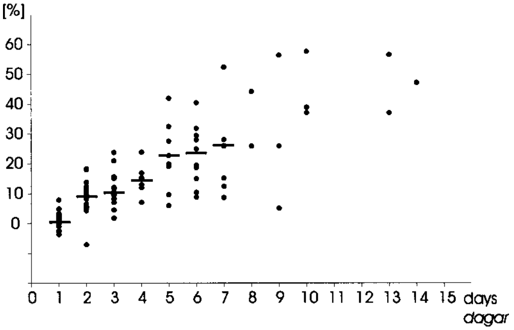

Figure 3. Relative body mass changes in juvenile Turnstones caught more than once. Horizontal lines indicate the mean value for a given day after the first capture.
Relativ förändring av kroppsvikten hos juvenila roskarlar återfångade olika antal dagar efter första fångsttillfället. De vågräta linjerna anger den genomsnittliga förändringen olika dagar efter märkningen.

The mean body mass of birds in the study area was low, like in African wintering grounds (Ens et. al. 1990), and only somewhat higher than recorded during breeding season (Glutz von Blotzheim et al. 1975). Turnstones, which are ready for long-distance flight, have body mass ranging between 120 and 200g (Gudmunsson et al. 1991). Bearing in mind all caveats concerning flight range estimates (Gudmunsson et al. 1991) and low average body mass of Turnstones caught in the Gulf of Gdańsk it appears that only the heaviest birds can reach northern Africa in one flight. The average body mass (99g) allows them to fly in one step at the most only to the North Sea coast or, when flying southwards over the mainland, to northern Italy. For more than 25% of Turnstones departing from the Gulf of Gdańsk the next stopover site is probably localised somewhere in the eastern Baltic, for example in the Mecklemburg Bay (450 km in straight line to the west), where three birds were caught 3, 3 and 9 days after ringing (Meissner & Koziróg 2000).

The mean body mass of juveniles increased during the season. Such phenomenon occurs also in other waders (Glutz von Blotzheim et al. 1975, Pienkowski et al. 1979, Meissner 1997a, 2000). Greater energy stores can be accumulated as an insurance when weather makes effective feeding impossible (Pienkowski et al. 1979). Indeed, in September the risk of facing severe weather is greater than in the summer months. However, another explanation to this phenomenon is possible; birds that encountered bad weather conditions stay longer at the study area. If they behave as time minimising migrants they could also accumulate larger fat reserves and thus gaining potential flight range. Unfortunately, the number of recoveries is too small to check this hypothesis.

The median length of stay of juvenile birds which stopped for more than one day in the study area (3.9 days) was similar to other wader species studied in the Gulf of Gdańsk (Krupa 1997, Meissner 1997b, Meissner & Włodarczak 1999, Meissner & Górecki in press). From the second day of stay the mean body mass increase was more or less stable and juvenile Turnstones that stayed longer also gained more energetic reserves. However, the majority of birds arrived with small fat reserves and departed after a very short stay. Only some of them stayed for several days, gaining about 50% of their initial body mass. Thus, the body mass at departure differed considerably among the migrants. The accumulation rate (calculated for the 3rd day of stay) was about two times and about 1.5 times higher than in juvenile Dunlin and juvenile Knots respectively (Meissner 1992, 1998b). Such high rate of the body mass increase (3.7%/day) was also found in Turnstone in September in Alaska (Thompson 1974 in: Zwarts et al. 1990).

Not all birds stayed in the study area for more than one day. Moreover, the number of adults, which stopped at the study area varied considerably between different seasons (Meissner & Koziróg 2000). It seems that the Gulf of Gdańsk is not a traditional stopover site for Turnstones, but it is probably a kind of emergency feeding place, like for Knots (Piersma et al. 1992) and for Sanderlings (Meissner & Włodarczak 1999). The body mass at departure varied considerably among juveniles. The number of recoveries is too small to investigate whether birds flying southwards over inland accumulate more energy reserves than those following seacoasts, where they can stop in many places en route. The decision to depart or to stay and gain body mass may be taken individually according to information gathered from the surrounding environment (the quality of a feeding ground, inter- and intraspecific competition for habitat resources, weather, predation pressure) and from its physiological stage (the amount of accumulated fat reserves and the rate of their accumulation) (Meissner 2001). Thus, the majority of birds behave as energy minimising migrants and migrate in small steps having low fat reserves. Others stay longer, gaining large energy reserves and probably they are able to reach North Africa in one step.

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Sammanfattning

En analys av biometriska data insamlade från roskarl Arenaria interpres *under höstflyttning i Gdanskbukten*

I denna studie har biometriska data från roskarl fångade i samband med ringmärkning under höstflyttningen i Gdanskbukten under åren 1983–1999 analyserats. Arten uppträder regelbundet, men i små flockar och antalet ringmärkta är lågt. Roskarlar som på hösten rastar i Gdanskbukten flyttar vidare i två riktningar, dels västerut till Atlantkusten och dels söderut över kontinenten till Medelhavet. Eftersom arten bara observeras i mindre antal i inlandet antas passagen av Europa ske genom en långflygning.

Roskarlarna har fångats vid tre olika platser: Jastarnia, floden Redas mynning och vid Rewa. Fältarbetet startade i mitten av juli och avslutades i slutet av september, en period som täcker så gott som hela artens flyttning. De mått som insamlats från de fångade individerna är vinglängd, huvud + näbblängd, näbblängd, tarslängd och tars + tålängd. Fåglarna vägdes också till närmaste gram. Totalt ingår 69 adulta och 389 juvenila fåglar i bearbetningen. Data från 67 juvenila fåglar som återfångats vid minst ett tillfälle under samma säsong har använts för att belysa fåglarnas viktökning under rastningen i området. Teoretiska beräkningar av flygsträcka har gjorts enligt Pennycuicks (1975) formel, även om senare rön har visat att denna formel troligen underskattar den sträcka en fågel kan flyga på en given energireserv.

Bland de insamlade måtten från de juvenila fåglarna är det bara vinglängd som uppvisar två distinkta toppar (Figur 1). Adulta fåglar hade en signifikant längre vinglängd än juvenila fåglar medan övriga mått inte skilde de båda åldersgrupperna åt. Bland de adulta fåglarna hade de som passerade före 24 juli en signifikant längre vinglängd och antas spegla honornas tidigare flyttningspassage. Någon liknande effekt kunde inte påvisas bland de unga fåglarna. Vikterna hos de juvenila fåglarna var signifikant högre i september jämfört med augusti (Figur 2).

Av de adulta fåglarna återfångades bara 2,8% (2 stycken) vid ett senare tillfälle samma höst medan samma siffra för ungfåglarna var 16,6% (67 stycken). Den genomsnittliga rastningsperiodens längd för de ungfåglar som återfångades var 3,9 dagar. Bland de återfångade fåglarna ökade vikten signifikant med tiden, även om en del fåglar minskade i vikt under de första dagarna (Figur 3). De som återfångades mellan två och sju dagar efter märkningen uppvisade en genomsnittlig ökning på 3,9g/dag och den genomsnittliga ökningen beräknad på de som kontrollerades efter tre dagar uppgick till 3,9% av ursprungsvikten/dag. Några juvenila fåglar stannade längre tid än en vecka och ökade i vikt med mer än 50% av ursprungsvikten. Den beräknade teoretiska flygsträckan för de tyngsta 10% (130–162g) uppgick till mellan 2500 och 3800 km. Den beräknade flygsträckan för fåglar som vägde 99g (den genomsnittliga vikten) var 1200 km och för de som vägde 88g (den övre gränsen för de 25% lättaste) var bara 480 km.

Den låga andelen återfångade individer i Gdanskbukten tyder på att majoriteten roskarlar inte stannar längre än en dag. Den lägre andelen återfångade gamla fåglar kan bero på att de är svårare att återfånga eller stannar kortare tid. Den lägre ökningen i vikt under den första dagen efter märkningen antas inte bara bero på hanteringen utan också på att fåglarna behöver genomgå en omställning innan de kan börja fettupplagra. Den genomsnittliga vikten var låg, snarlik den hos fåglar under vintern i Afrika och bara något högre än under häckningstid. Roskarlar som står i begrepp att genomföra långdistansflygningar har normalt vikter mellan 120 och 200g, vilket antyder att bara ett fåtal av fåglarna i Gdanskbukten kan nå Nordafrika i en flygetapp. Fåglar med genomsnittlig vikt kan nå Nordsjökusten i väster och om de flyger söderut norra Italien. För närmare 25% av fåglarna ligger förmodligen nästa rastplats i sydvästra Östersjön, till exempel i Mecklenburgbukten (450 km västerut), där också tre fåglar kontrollerats 3, 3 och 9 dagar efter märkningen. Att vikten ökar med säsong, vilket också påvisats hos flera andra vadararter, kan vara en försäkring mot dåligt väder då möjligheten till födosök kan vara försämrad. En annan möjlighet kan vara att fåglar som senare under hösten möter sämre väder stannar längre tid och lägger upp en större energireserv. Resultaten antyder att Gdanskbukten inte är en traditionell rastplats för roskarl utan snarare fungerar som en plats att nyttja i nödfall, vilket också visats för kustsnäppa och sandlöpare. Variationen är dock stor och även om huvudparten beter sig som energiminimerare som bara lägger upp små energireserver och flyger kortare sträckor, så finns det en del som lägger upp mycket stora reserver som gör det möjligt för dem att nå Nordafrika i en flygetapp.

Nya böcker *New books*

Olof Dixelius, 2000: **Linnétraditionen i svensk litteratur. En kritisk granskning.** Kungl. Vitterhets Historie och Antikvitets Akademien. 64 sid.

Som nummer 41 i Kungl. Vitterhets Historie och Antikvitetsakademiens skriftserie "Filologiskt arkiv" publicerar Olof Dixelius sin studie över vilken betydelse Carl von Linné har haft för naturskildringen i Sverige. Han går igenom en lång rad författare från 1700-talet och fram till vår egen tid i syftet att finna stildrag som kan kallas linneanska. Som han själv påpekar är uppgiften svår att utföra, inte minst därför att en modern metoddiskussion på området saknas. Dixelius hänvisar ganska ofta till Knut Hagbergs flera årtionden gamla texter i ämnet. Hagberg skrev utmärkt om Linné men gav ofta efter för en tämligen devot beundran och var enligt mitt sätt att se det ibland ganska långsökt i sin strävan att tillskriva Linné förtjänster av alla möjliga slag. Dixelius betonar att Hagberg var en populärförfattare på området. Möjligtvis är detta en sorts reservation. Själv anför Dixelius bland annat nyfikenheten på naturen och intresset för detaljerna som typiska för Linnés stil. Detta kan vi hålla med om men frågan kvarstår om det finns influenser från Linné så fort vi träffar på detta hos senare naturskildrare. Jag känner mig inte säker på det.

Den här recenserade skriften ger en god överblick över svenska författare som ägnat sig åt naturmotiv men själva ambitionen att visa på Linnés betydelse för deras stil är inte övertygande genomförd. Undertiteln, "en kritisk översikt", är knappast motiverad. Den påverkan från Linné som antyds är inte på något sätt självklar och behöver nog granskas mer ingående. För övrigt frågar jag mig, gamle Linnéläsare, hur intressant detta egentligen är. I själva verket torde kärlek till friluftsliv, häpnad över kuriösa företeelser och fascination inför fåglar och djur ligga i naturstudiets karaktär, vara själva saken. Senare naturskildrare som t. ex. Erik Rosenberg, vilken nämns här, har sannolikt känt detta alldeles oavsett eventuell påverkan från Linné. När han som tonåring betraktade Kvismarens kärrhökar med oförställd blick säger det förmodligen mer om honom själv än om hans eventuella bekantskap med Linnés skrifter. Riktigare är nog att betrakta både Rosenberg och Linné, liksom många andra av våra författare med naturmotiv, som självständiga och lyhörda skildrare av svensk fauna och flora. Var och får sin egentliga kvalitet genom att han ej kan härmas, var och är omistlig genom att han lagt sitt perspektiv till vår gemensamma litteratur. Också Gunnar Brusewitz som Dixelius anser vara en eminent länk i Linnétraditionen, "… hos honom löper trådarna ovanligt väl samman, … ögats genialitet, känslan för det stora i det lilla, saklighet …", finner jag huvudsakligen självständig.

Linné tillhör vår idé- och lärdomshistoria och senare författare kan säkert granskas utifrån frågeställningen hur deras natursyn har influerats av Linné. Hans syn på naturen, liksom hans samtids, var som bekant teleologisk, den var ändamålsbestämd och dess vägar var utstakade av en outgrundligt vis skapare. Han kunde uttala sig på ett sätt som för tankarna till mystik och panteism men också på ett sätt som föregrep senare tiders ekologiska tänkande. I det senare hänseendet kunde man kanske finna tankegångar och uttryck som färgats av vår store naturalhistoriker på 1700-talet. Annars har det mesta i hans föreställningsvärld ändrats efter Darwin.

Våra tiders naturskildrare kan känna till och beundra Linné, att vara hans lärjungar måste te sig svårare. Som flitig läsare av ovannämnde Brusewitz har jag t. ex. svårt att uppfatta hans natursyn som bestämd av Linnés. Hans förhållningssätt till Linné är i mina ögon distanserat och hans stora Linnékunskap har knappast lagt band på hans egen originalitet. Att han gärna hänvisar till Linné är en annan sak. Hans utgångspunkter är dessutom många fler. Nå, det vore kanske bäst att fråga Gunnar Brusewitz själv om det.

Jag finner att jag här har ifrågasatt förfärligt mycket av det som Olof Dixelius velat visa med sin lilla avhandling. Därför måste jag skynda mig att tillägga att jag inte tycker den är oviktig eller att den inte förtjänar att läsas. Dess teser övertygar mig inte men den får absolut stå på hyllan för "Linneana".

BO EKBERG

Daniel C. Dennet, 2000: **Att förstå medvetandet hos människor och andra djur.** Natur & Kultur, serien Science Masters. 183 sid.

Ju längre den vetenskapliga forskningen sträcker sig, desto större blir behovet av överblick. Därför förtjänar ett arbete av en filosof och kognitionsforskare att omnämnas även i en ornitologisk tidskrift. Ta till exempel beteendeekologin som för närvarande är ett dynamiskt arbetsfält för forskarna. Bakom det som synes ske i djurpopulationer framträder mönster för vad som verkligen sker. För att göra detta mönster åskådligt behövs dels en teori, dels en framställningsform som refererar till sådant som kan förstås med utgångspunkt från vardagliga referensramar. När till exempel fortplantningsstrategier hos olika fågelarter undersöks används som vi vet ett antropomorft uttryckssätt. Aktörerna beter sig på ett sätt som förefaller vara beräknande, intentionellt som filosoferna säger. Med taktiskt raffinemang strävar de efter att ge upphov till så stor fortplantningsduglig avkomma som möjligt. I arsenalen av knep och finter ingår såväl lögnaktiga beteenden som skryt och skrävel som moraliskt ljusskygga övningar i stil med utomparskopulation i obevakade ögonblick. Kartlägger man det samlade uppträdandet hos en viss individ under en häckningssäsong och skildrar det enligt sin teori på mänskligt språk framstår alltihop som begripligt.

Naturligtvis finns risken att man vandrar vilse. Ett framgångsrikt beteende vilket premieras av selektionen kan lätt börja framstå som medvetet, övervägt. För att undgå ett sådant misstag blir det nödvändigt att lägga in reservationen att djuret endast handlar *som om* den visste vad den gjorde. Därigenom markerar man att det *egentligen* inte är på det viset, det är bara ett sätt att uttrycka saken. Bakom alltihop verkar i stället någon annan sorts mekanism som styrande faktor. Genom denna "förstår" fågelindividen att välja bäst revir, gynnsammast partner och mera sådant som är bra för den egna avkomman, d.v.s. för ens gener.

När man använder en framställningsform som baseras på analogier från människans värld är det viktigt att poängtera detta. Därigenom gör man klart att man inte vill tillskriva djur och andra organismer mänskliga föreställningar. För undvikande av missförstånd. En fara som i stället dyker upp är risken att reducera människor till djur. När man har beskrivit djurens beteenden med mänskliga termer har man ju visat att de gör likadant som människorna. När man sedan förklarar att detta görs via någon sorts omedveten automatik är det lätt att få för sig att det förhåller sig likadant bland människorna. *Prunella modularis* eller *Homo sapiens,* kanske kvittar det lika?

Om man har en känsla av att det ändå inte är riktigt på det viset måste man börja fundera över medvetandets märkliga natur. Att kalkylera och därmed riskera att felkalkylera. Att formulera mål och bygga ideologier. Daniel C. Dennet är en filosof som har ägnat sig åt frågor kring medvetandefunktionen. Att han är en tänkare som väckt intresse bland biologer framgår av att han diskuteras i arbeten som till exempel Andrew Browns *The Darwin Wars* och Richard Dawkins´ *The Selfish Gene,* andra upplagan. Därmed kan han kanske också vara av intresse för denna tidskrifts läsare.

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Allmänt gäller att bidrag skall vara avfattade enligt den modell som finns i tidigare häften av tidskriften. Titeln skall vara kort, beskrivande och innehålla ord som kan användas vid indexering och informationssökning. Uppsatser, men ej andra bidrag, skall inledas med en Abstract på engelska om högst 175 ord. Texten bör uppdelas med underrubriker på högst två nivåer. Huvudindelningen bör lämpligen vara inledning, metoder/studieområde, resultat, diskussion, tack och litteratur. Texten får vara på svenska eller engelska och uppsatsen skall avslutas med en fyllig sammanfattning på det andra språket. Tabell- och figurtexter skall förses med översättning till det andra språket. Tabeller, figurer och figurtexter skall finnas på separata blad. Det skall finnas minst 4 cm marginal till vänster om texten som skall vara utskriven med minst dubbelt radavstånd. Manus skall insändas i tre kopior inklusive tabeller och figurer. *Såväl text som figurer skall om möjligt levereras på diskett.*

Andra bidrag än uppsatser bör ej överstiga 2 000 ord (eller motsvarande om det ingår tabeller och figurer). De skall inte ha någon inledande Abstract men däremot en kort sammanfattning på det andra språket.

Författarna erhåller korrektur som skall granskas omgående och återsändas. Av uppsatser, men ej övrigt, erhåller författaren 50 särtryck gratis.

Referenser skall i texten anges med namn och årtal samt bokstäver (a, b etc) om det förekommer referenser till samma författare och år mer än en gång. För litteraturlistans utformning se nedan.

Contributions should be written in accordance with previous issues of the journal. The title should be short, informative and contain words useful in indexing and information retrieval. Full length papers, but not other contributions, should start with an Abstract in English not exceeding 170 words. The text should be divided by no more than two levels of subheadings. The following primary subheadings are recommended: Introduction, Methods/Study areas, Results, Discussion, Acknowledgements, and References. The text may be in English or Swedish and the paper should end with a comprehensive summary in the other language. Table and Figure legends should be in both languages. Tables and Figures must be on separate sheets of paper. Manuscripts should be submitted in three copies with at least 4 cm margin to the left, printed with at least double line spacing. Text and figures should preferably be provided on a floppy disk.

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Authors will receive proofs that must be corrected and returned promptly. Fifty reprints of full length papers, but not of other contributions, will be free of charge.

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Referenser *References*
I texten *In the text*: Andersson (1985), Bond (1913a, 1913b), Carlsson & Dennis (1956), Eriksson et al. (1989), (Andersson 1985), etc.

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