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Molt stage, wing bar patterns and digital photography as tools for assessing age distribution and recognizing individuals of Great Grey and Snowy Owls

PhD in Applied Ecology and Biotechnology
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Preface

My interest for owls started shortly after birds captured my fascination, when a small Pygmy Owl perched in a birch tree outside my classroom window. I was twelve, I was lost, and I have been lost to the world of owls ever since. I have been fortunate to meet all ten species of owls which regularly breed in Norway, and have had the opportunity to study several of them at close range.

Since 1995 I have been employed as a Senior Curator in Zoology at the Agder Natural History Museum in Kristiansand, which in 2017 became an integrated university museum under Agder University. My position has made it possible to work in the border zone between life and death, combining studies of free living owls with skin studies in scientific museum collections. I am grately indepted for the opportunity my employers have granted me for these studies, and finally giving me time to compile my work into this PhD thesis.

Petter Wabakken at Evenstad, Inland Norway University, has been a great friend and ispirator for many years, and we have shared passion and fascination for wildlife since our student days at the University of Oslo. He strongly urged me to apply for the PhD studies at Evenstad, and I am very thankful for his thrust, and interest in my work. This PhD might never have seen the light of day without him.

I also wish to thank Evenstad for taking me in as a PhD candidate. It has been a pleasure to return to student mode, follow courses and get to know the other PhD-students, professors and teachers. The staff at Evenstad have been very nice, and I have always felt welcome at this campus. I especially thank Kjartan Østbye for accepting an old «dinosaur» among his PhD-students.

I thank all the museums which granted me access to their skin collections; Tromsø Museum, Bergen Museum, Natural History Museum in Oslo (former Zoological Museum Oslo), Swedish Natural History Museum in Stockholm (NRM), Helsinki Museum, Copenhagen Zoological Museum, Smithsonian Museum in Washington and the Natural History Museum in New York. I also thank the many people who kindly helped me at these museums.

The material from the field studies could not have been collected without the help of many co-workers and friends. I first thank my colleagues and co-researchers in the Norwegian Snowy Owl Project: Karl-Otto Jacobsen, Ingar Jostein Øien and Tomas Aarvak, with whom I have shared many magnificent and exclusive owl moments! My co-workers of Snowy Owl studies in Canada and USA collected a vast number of wing images of Snowy Owls captured on the great prairies. These images have been paramount to untangle the moult sequences

for aging Snowy Owls. I am thus greatly in debt to Tom McDonald, Dan Zazelenchuk, Mike Blom and Marten Stoffel who sent me photos. Karen Wiebe at the Saskatoon University has also been a valuable co-worker in the Snowy Owl studies. I also thank Aleksandr Sokolov for letting me use his owl images from Beliy Island in 2015 to test the applicability of my methods on Snowy Owls, and for co-authoring paper IV.

Each spring brings excitement and high hopes, as field season and time to inspect the owl forests in Hedmark, Värmland and Dalarna approaches. Steinar Myhr has been my close associate and co-worker on most of this field work since 2008, and has been of great help and support. We have shared many exciting and splendid moments in the boreal forests of central Scandinavia, and I am very thankful for his company and friendship.

Many ornithologists have shared information and work on the Great Grey Owl adventure in Hedmark. Trond Berg has collected the majority of wing images of captured owls, and also compiled the nest data into readable Excel-sheets. I am very thankful for his cooperation and field efforts. Many people have contributed with localities and information on the Great Grey Owls. With the danger of missing someone I would especially thank the support provided by Roar Svenkerud, Steinar Kråbøl, Carl Knoff, Rune Bjørnstad, Robert Huldt and Egil Østby.

Antonio B. S. Poleo at Evenstad helped me arrange the blind test of Great Grey Owl wings. Kjartan Østbye and Geir A. Sonerud have kindly read and given valuable comments to the PhD synopsis. I am grately thankful for their corrections and support. Geir A. Sonerud also co-authored paper V on the Great Grey Owl age studies in Hedmark, and greatly enhanced the quality of this paper. I am very thankful for his help, lifelong friendship and shared fascination for owls.

Roar Solheim
Grimstad and Evenstad
September 2019

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Contents (continued)

Sammendrag (Norwegian summary)

Det blir varmere. Klimaet er i endring, og endringene gir størst utslag på nordlige breddegrader. Økosystemene i tundra og taiga-sonene er dermed også gjenstand for endringer, selv i fjerntliggende områder hvor mennesker sjeldent ferdes. Ett av særtrekkene ved disse nordlige økosystemene er regelmessige svigninger i bestandene av både pattedyr, fugler og insekter, med smågnagere som sentrale nøkkelarter i dynamikken. Flere studier har vist endringer i syklisiteten til smågnagere de siste tiårene, med konsekvenser for mange arter i næringsnettet. I første rekke forventes endringer i smågnagernes syklisitet å påvirke smågnagerjegere. Alle arktiske og boreale uglearter jakter smågnagere, og arter som snøugle og lappugle er helt avhengige av disse byttedyrene for å kunne hekke. Snøugla er listet som sårbar på verdensbasis, mens verdensbestanden av lappugle er klassifisert som stabil. I Fennoscandia har hekkeutbredelse og bestandsstørrelse for snøugle avtatt, mens lappugla nylig har ekspandert som hekkefugl.

Som smågnagerjegere er snøugle og lappugle direkte påvirket av smågnagersvigningene. Forskjellen i bestandsutvikling for disse to smågnagerspesialistene i Fennoscandia gjør det spesielt interessant å overvåke deres bestandsutvikling i lys av eventuelle endringer i smågnagernes syklisitet. Slik overvåking krever kunnskap om artenes bestandstørrelse, reproduksjon og overlevelse, og kjennskap til aldersstruktur i en bestand er fundamental informasjon, siden reproduksjon og dødelighet varierer med individenes alder. Mytemønstre er essensiell kunnskap for å kunne aldersbestemme mange fugler. Hos arter hvor juvenile og adulte fjær er forskjellige kan dette brukes for å aldersbestemme fugler fanget for ringmerking.

I denne avhandlingen presenterer jeg en metode for å kunne aldersbestemme lappugler og snøugler basert på mytemønster i fuglenes vinger. Jeg har vist hvordan forskjeller på fuglenes første sett av juvenile vingefjær skiller seg fra neste sett av adulte vingefjær, og at det tar tre til fire år før alle juvenile vingefjær er skiftet ut. Så lenge noen juvenile fjær fremdeles er tilbake i vingene, er det som regel mulig å se hvor mange fjærskifter fuglene har gjennomgått siden de ble klekket, og dermed også bestemme fuglens alder. Jeg har også vist hvordan flekkmønster i fuglenes vingefjær kan brukes til å gjenkjenne individer og å skille mellom forskjellige fugler. Ved hjelp av fotografier av lappugler og snøugler i flukt er det også mulig å foreta aldersbestemmelse og identifikasjon av frittflyvende ugler uten å fange dem inn. Slik individgjenkjenning uten innfanging og merking har lenge vært benyttet på pattedyr, men har tidligere ikke blitt brukt på frittflyvende fugler. Bruk av fotografering for å gjenkjenne eller skille mellom individer representerer en ikke-invasiv teknikk som også kan øke mengden av data i bestandsstudier av fugler. Metodene for aldersbestemmelse og individgjenkjenning har blitt anvendt i tre ulike studier av snøugle og lappugle.

Under en sommerinvasjon av snøugler på Beliy øya nord for Yamalhalvøya i Russland i juli 2015, ble så mange snøugler som mulig fotografert langs fire takseringsruter på tundraen. Ved å sammenligne flekkmønster i uglenes vinger ble et minimum på 25 ugler identifisert for kjønns- og aldersbestemmelse. Mytemønster i vingene viste at 80% av fuglene var klekket i årene 2012-14. Sammenholdt med bevegelsene hos 12 voksne snøugler som ble satellitt-merket på hekkeplass i Norge i 2011 viste materialet at det må ha funnet sted vellykket hekking flere steder langs arktisk tundra i Russland i flere av årene 2012-14.

Bestanden av hekkende lappugler ble fulgt i Hedmark fra 2009-2018, da antallet hekkefugler økte fra ett par til 119 par i 2017. Voksne hekkefugler ble fanget inn for ringmerking eller kontroll, og deres vinger ble fotografert for aldersbestemmelse ved hjelp av mytemønster i vingene. Fugler som ikke lot seg fange ble forsøkt fotografert i flukt. Dette økte mengden tilgjengelig materiale, spesielt for hanner som er vanskeligere å fange på reirplass enn hunner. Året 2011 med 22 hekkefunn skilte seg ut, da hele 77% av hekkefuglene var ungfugler klekket i 2010. Aldersbestemmelse og gjenfunn av fugler ringmerket som reirunger i midt-Sverige viste at lappuglenes etablering av en hekkefuglbestand i Hedmark skyldes spredning av ungfugler etter et godt hekkeår i Sverige i 2010.

I det siste studiet har jeg vist hvordan opplysninger samlet inn av publikum (public sciences) kan anvendes for å aldersbestemme lappugler når de jakter i åpent landskap under et smågnagerbunnår. I løpet av 2012 ble mer enn 4000 enkeltrapporter om snøugler lagt inn i artsdatabanken, hovedsakelig i Sverige. Litt over 800 av rapportene var ledsaget av bilder av den observerte lappugla, hvorav 323 kunne brukes til å aldersbestemme fuglen. Ved hjelp av lokalitetenes ID-numre ble antallet lappugleindivider redusert til 144 fugler. Aldersbestemmelse ved hjelp av fjær viste at minst 76% av fuglene var ungfugler klekket i 2011, noe som viste at også dette året var et godt reproduksjonsår for lappugler i Sør-Skandinavia.

Abstract

The world is heating up. The climate is changing, with increasing temperature changes towards the Arctic. Northern ecosystems of tundra and taiga are subject to changes, even in the most remote areas void of human presence. One of the most profound characteristics of these northern ecosystems are the cyclic changes in population size of mammals, birds and insects, small microtine rodents being the central species in the dynamics. Several studies have demonstrated that the cyclicity of lemmings and voles have changed during the recent decades, with consequences for many other species of the food webs. Changes in the cyclicity of lemmings and voles are especially expected to influence their predators. All arctic and boreal owl species hunt microtine rodents, and species like the Snowy Owl and the Great Grey Owl are totally dependent on such prey animals to breed. The Snowy Owl is listed as a vulnerable species worldwide, while the Great Grey Owl is considered to have a stable world population. The population of Snowy Owls breeding in Fennoscandia has declined while the Great Grey Owl recently has expanded its breeding distribution.

Small mammal hunters like the Snowy Owl and the Great Grey Owl are directly influenced by changes in the cyclicity of microtines. The difference in population development of these two vole hunters in Fennoscandia enhance the importance of monitoring both species under a regime of expected future changes of ecosystem cyclisity. Knowledge of population size, reproduction and survival, and the age structure of populations are paramount information in such monitoring because reproduction and mortality varies with age. Moult patterns are essential for aging many birds. In species where juvenile and adult feathers look different, such differences can be used for aging a bird when it is captured for banding.

In this thesis I present a method for aging Great Grey Owls and Snowy Owls based on the moult patterns in their wings. I have demonstrated the difference between the first juvenile wing feathers and later adult wing feathers, and that it takes three to four years for an owl to replace all juvenile wing feathers. As long as at least one juvenile wing feather is left in the wing, the number of moults and the age of the owl can usually be determined. I have further developed a method for individual identification of Great Grey Owls and Snowy Owls based on bar patterns of their wing feathers. I have shown that it is possible to use photographs of free flying owls for aging and identification of individuals. Identification based on visible characters is a long established and used technique in studies on mammals, but has hitherto not been used on free flying birds. Using photographs in such studies is a non-invasive technique which may enhance the amount of data available in population studies of birds. I have used these techniques in three studies on Snowy Owls and Great Grey Owls.

Snowy Owls were photographed along transect routes during a summer invasion on Beliy Island north of the Yamal Peninsula in Russia in July 2015. A minimum of 25 owls were identified, sexed and aged by studying the moult and bar patterns of their wings from photos of owls in flight. The moult patterns showed that 80% of the owls were hatched in 2012-14. Results from Norwegian satellite studies of Snowy owls showed that 12 adult owls which bred in Norway in 2011 spent the summers 2012-14 along the Russian Arctic. This implies that Snowy Owls must have bred successfully in these parts of the Russian Arctic in 2012-14.

An expanding population of Great Grey Owls was studied in Hedmark county, south-eastern Norway in 2009-2018, when the number of recorded nestings rose from 1 to 119. Adult breeding owls were captured for banding or control, and their wings were photographed for moult analyses and aging. Birds which could not be captured were photographed in flight. The photographic method increased the amount of birds which could be aged, and especially the amount of males which may be more reluctant to approach intruders at the nest site, and thus avoid capture. In 2011 no less than 77% of the recorded breeding Great Grey Owls were young birds hatched the previous year. Control of two nesting Great Grey Owls banded as nestlings in Sweden in 2010 indicated that good reproduction in mid-central Sweden in 2010 followed by natal dispersal of young birds was the foundation of the breeding population in Hedmark.

I have demonstrated that data gathered through public sciences can be used to age Great Grey Owls when they hunt in open landscapes outside the breeding range during a vole depression year. More than 4000 reports of Great Grey Owls were received through the national species archives in Norway and Sweden in 2012, the majority of data derived from Sweden. Slightly more than 800 of these reports were accompanied by photo(s) of the owl, and of these 323 could be used to age the bird. The number of individuals was reduced to 144 by the ID number of localities, because one owl may be reported by different observers. Wing and tail feathers showed that at least 76% of all the Great Grey Owls reported in 2012 were juvenile birds hatched in 2011. This demonstrated that also 2011 was a good reproduction year of Great Grey owls in south Scandinavia.

Keywords:
Strix nebulosa, *Bubo scandiacus*, moult sequences, aging, individual identification, age structure, population changes, public sciences.

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PAPERS

This thesis is based on the following original papers and one manuscript (V), which are referred to by Roman numerals.

I Solheim, R. 2011. Molt pattern of primaries and secondaries during first and second flight feather molt in Great Grey Owls *Strix nebulosa*. Ornis Svecica 21:11-19.

II Solheim, R. 2012. Wing feather moult and age determination of Snowy Owls *Bubo scandiacus*. Ornis Norvegica 35: 48-67.

III Solheim, R. 2016: Individual identification of Snowy Owls (*Bubo scandiacus*) and Great Grey Owls (*Strix nebulosa*) based on wing bar patterns. Journal of Raptor Research 50 (4): 370-378.

IV Solheim, R. & Sokolov, A. (in print). Age and sex of Snowy Owls *Bubo scandiacus* during summer irruption on Beliy Island, Yamal in 2015. Airo.

V Sonerud, G. A., Solheim, R., & Berg, T. (manuscript): Age structure in a newly established and expanding population: high proportion of young individuals among nesting Great Grey Owls.

VI Solheim, R. 2014: Age of Great Grey Owls *Strix nebulosa* observed in Scandinavia in 2012 as revealed by digital photos in the national species report archives. Ornis Svecica 24: 3-11.

1. Introduction

The world´s climate is changing (Allen et al. 2018), and climate change is believed to be a major threat to essential ecosystem functions like the cyclic fluctuations of vole and lemming populations of northern taiga and tundra (Cornulier et al. 2013). Reproduction of many raptors and owls are directly linked to the cyclicity of these small rodents (Hagen 1952), and changing populations of vole specialist hunters may thus reflect changes in these basic population cycles. The Snowy Owl *Bubo scandiacus* and the Great Grey Owl *Strix nebulosa* are specialist vole hunters of tundra and taiga (Mikkola 1983, del Hoyo 1999). While the population of nesting Snowy Owls has decreased in Fennoscandia the last 40-50 years (Solheim 2004, Jacobsen et al. 2014), the Great Grey Owl has recently expanded its distribution to south eastern Norway (Solheim 2009, Berg et al. 2011, 2019). Demographic information like productivity and survivorship are fundamental parameters to understand when and which factors causing declines or increases i bird populations occur, and information on the age of individual birds studied are essential for such studies (Pyle et al. 2008). Moult and wear of feathers are the essential cues for aging birds which have not been banded as nestlings (Svensson 1992, Jenni & Winkler 1994, Pyle et al. 2008). Climatic conditions may also have a direct effect on moult (Zuberogoita et al. 2016). According to a recent review on studies of moult in birds of prey, there is still a huge lack of basic knowledge on this topic, and the authors stress moult as a future tool that can be used to complete the information necessary for understanding the life of birds of prey (Zuberogoitia et al. 2018).

1.1 Snowy Owl and Great Grey Owl – the species

The Snowy Owl and the Great Grey Owl are among the largest owl species on the northern hemisphere, only surpassed in size by the Eurasian Eagle owl *Bubo bubo*, the Great Horned Owl *Bubo virginianus* in North America and the Blackiston´s Eagle Owl *Bubo blakistoni* in Japan and eastern China and Russia (del Hoyo 1999). While the latter three species are mostly active during night and seldom seen by people, the Snowy Owl and the Great Grey Owl can hunt also during daytime. Both species are often observed by humans where they appear, and usually draw a lot of attention from bird-observers, nature photographers and ornithologists, and also from the general public. They stand out as both enigmatic and iconic birds of northern tundra and taiga. While the Snowy Owl is classified as a vulnerable species (IUCN 2017), the Great Grey Owl is classified as a species of least concern (IUCN 2017), and has recently expanded its distribution in NW Europe (Ławicki et al. 2013).

The Snowy Owl is the only owl species where males and females look different and can be sexed based on plumage alone (Mikkola 1983, Olsen & Fredriksson 1992). It has a Holarctic distribution, and breeds in treeless tundra and mountainous regions in Fennoscandia, Russia, Alaska, Canada and Greenland (Portenko 1972, Cramp 1985). Based on genetic studies, Marthinsen et al. (2009) concluded that the Snowy Owl make up one panmictic population with gene flow around the Holarctic range of the species.

The Great Grey Owl is divided in two distinct subspecies; *Strix nebulosa nebulosa* in North America and *Strix nebulosa lapponica* in Eurasia (Mikkola 1983, del Hoyo 1999). These subspecies seem primarily to differ with respect to plumage colouration, while size and behaviour are strikingly similar on both continents (Mikkola 1983).

Snowy Owls and Great Grey Owls can appear outside their breeding ranges in considerable numbers, described as irruptive migration or nomadism (Portenko 1972, Mikkola 1983, Newton 2008). Studies of adult Snowy Owls equipped with satellite transmitters have revealed that they may move up to 3000 km from one year to the next (Fuller et al. 2003, Solheim et al. 2008, Jacobsen et al. 2012, 2017, Therrien et al. 2014), and between summer and winter ranges (Solheim et al. 2014, Doyle et al. 2018, Øien et al. 2018). Controls of banded breeding Great Grey Owls have revealed movements of up to 101 km between breeding locations in Sweden (Solheim & Stefansson 2016) and 405 km in Finland (Valkama et al. 2014). North American Great Grey Owls tracked with radio-telemetry moved up to 325 km (males) and 684 km (females) from one breeding home range to the next (Duncan 1987). Recent studies of Great Grey Owls with satellite transmitters have revealed post-breeding movements between consecutive nesting seasons of 645 km and 1300 km (Solheim et al. unpubl. data). Mean natal dispersal for Great Grey Owl females in Sweden was 40 km (Solheim & Stefansson 2016), and in Finland 48 km (Valkama et al. 2014). In Sweden the mean natal dispersal distance was linked to the age of the female owl at first control, varying from 7 and 115 km (Solheim & Stefansson 2016).

1.2 Population status of the Snowy Owl and the Great Grey Owl

1.2.1 Snowy Owl

The Snowy Owl world population was formerly estimated to 290 000 – 300 000 individuals, based on national figures which in turn is derived from qualified guesses on maximum number of breeding birds (Rich et al. 2004, Birdlife International 2013). Based on DNA studies the effective population size was estimated to be as low as between 1 700 and 14 100 reproductive females (Marthinsen et al. 2009), corresponding to a world population of maximum 30 000 Snowy Owls (Jacobsen et al. 2014). Results from the satellite studies since 2007 seem to support that the world population of Snowy Owls may be as low as these estimates indicate, because the same owls may have been counted several times when moving between countries. Consequently the Snowy Owl was recently reclassified from species of least concern to vulnerable (IUCN 2017).

In Norway the Snowy Owl was a regular breeder as far south as the Hardanger mountain plateau until 1974, when only one nesting pair was found (Solheim 2004). During the first half of the 1900eds and until 1959 more than ten pairs were known to nest in the lemming peak years in this southern range of Fennoscandia. At least seven nests were recorded on the Hardanger mountain plateau in 1963, but between this year and 1974 no more than one nest was found there in any year (Solheim 2004). The best breeding year ever documented for Snowy Owls in Fennoscandia was 1978, when as many as 200 pairs may have nested in Northern Fennoscandia, primarily in Sweden (Wiklund & Stigh 1986, Lindberg & Wiklund 1991). At least 22 nests were reported from Northern Norway this year (Jacobsen 2005). In 1985, 20 nests were reported from mid-central Norway (Nordland county; 19, Trøndelag county; 1; Jacobsen 2005). In 2011, 42 nests or nesting attempts were recorded in Norway, which is so far the highest numbers of Snowy Owl nests ever recorded in one year in Norway (Jacobsen et al. 2012). At least 54 nests or nesting attempts were recorded for Norway, Sweden and Finland pooled this year (Jacobsen et al. 2012). Snowy Owls nested in Fennoscandia again in 2015, when 50 nests were reported (23 in Norway; 23 in Sweden and 6 in Finland; Øien et al. 2016). Although around 50 nests were recorded in Fennoscandia in the years 2011 and 2015, the total number of nesting Snowy Owls is reduced since 1978. Also the breeding range of the species has diminished, since Snowy Owls have been confined to the northernmost part of their former breeding range in Fennoscandia since 1974 (Jacobsen et al. 2014).

1.2.2 Great Grey Owl

The Great Grey Owl expanded its breeding range southwards in Sweden from the mid 1980s (Stefansson 1997, Svensson et al. 1999). In Norway, one nest was found in Trysil municipality, Hedmark county in 1989 (Foyn & Blestad 1989), and the next in Sør-Odal municipality, Hedmark county in 2009 (Sagen & Sagen 2009). Sightings of Great Grey Owls became increasingly more regular in Hedmark county from 1989 to 2009 (Solheim 2009). During the ten years following 2009, the Great Grey Owl literally «exploded» as a breeding species in Hedmark county, where as many as 119 nests were recorded in 2017 (Berg et al. 2019). Interestingly the Great Grey Owl had a similar expansion in a south-westerly direction from Russia to the Baltic nations, Belarus and Poland during the same time period (Ławicki et al. 2013).

The total Swedish population of nesting Great Grey Owls was judged to have declined from 500 to 400 pairs during 1980-2010 (Hipkiss et al. 2008, Ottosson et al. 2012), while the population was deemed stable in Finland, fluctuating between 300 and 1500 nesting pairs (Valkama et al. 2011).

The North American population of the subspecies *Strix nebulosa nebulosa* is estimated at minimum 50 000 individuals (del Hoyo et al. 1999). The species´ distribution extends southward along the Rocky mountains into California, where it was listed as an endangered species in 1980 (Wu et al. 2016). Very little is known about the world population size of the Eurasian subspecies *S. n. lapponica* outside of Fennoscandia (Cramp 1985, del Hoyo 1999). IUCN (2017) gives an estimate of the total world population between 50 000 and 100 000 individuals. It is classified as a species of least concern, and the current population trend (worldwide) is judged to be increasing (IUCN 2017).

1.3 Prey choice

To breed successfully both Snowy Owls and Great Grey Owls depend on microtine rodents such as lemmings and voles (Portenko 1972, Stefansson 1997). Lemmings *Lemmus* and collared lemmings *Dicrostonyx* seem to be the most important small mammals determining Snowy Owl breeding success (Cramp 1985), locally supplemented with *Microtus* and *Myodes* vole species (Løvenskiold 1947, Hagen 1960). Worldwide the breeding range of the Snowy Owl on large coincides with the distribution of lemming species (Potapov & Sale 2012). Exceptions are a few nesting occasions on Iceland (Stenkewitz & Nielsen 2019) and Shetland (Tulloch 1968), where the owls hunted grouse, ducks, seabirds and rabbits (Shetland). If populations of lemmings and voles crash during the breeding season, Snowy Owls switch prey from mammals to birds (Cramp 1985, Potapov & Sale 2012). Snowy Owls are agile aerial hunters, able to capture birds on the wing (Tulloch 1969, own observations). Avian prey in Snowy Owl breeding areas range from passerines and waders to auks, gulls, ducks and grouse (Smith 1997, Potapov & Sale 2012, Øien et al. 2016). In winter, Snowy Owls readily hunt large prey such as ducks, grouse, rabbits and hares (Campbell & MacColl 1978, Danilov et al. 1984). Large prey such as Canada Goose *Branta canadensis* and Great Blue Heron *Ardea herodias* have also been recorded (Smith 1997). Recent satellite studies have revealed that Snowy Owls during winter choose different strategies and hunting habitats. Some owls stay in the Arctic, hunting seabirds in the drift-ice or ptarmigans on land (Therrien et al. 2011, Doyle et al. 2017, Øien et al. 2018), while others migrate southwards to open prairie grasslands (Solheim et al. 2014). During winter Snowy Owls may also turn up in coastal wetlands and river deltas and hunt a large variety of birds (Smith 1997, Smith et al. 2012).

Great Grey Owls hunt almost exclusively microtine voles, and seem to select *Microtus* and *Myodes* species up to 50 g size (Mikkola 1983). Even when larger prey such as water voles (*Arvicola terrestris*) are present, the owls seem to avoid them and prefer the smaller voles (Höglund & Lansgren 1968, Mikkola 1983, Stefansson 1997, Kropacheva et al. 2019). In a study of Great Grey Owls *S. n. nebulosa* in the Yukon area, microtine rodents made up 94% of the diet by number (Osborne 1987). Although shrews *Sorex* spp. made up 39.4% of 221 mammals caught in trap lines in this study, the owls seemed to avoid this kind of prey, as only one shrew was found among the 411 prey animals.

1.4 Hunting behaviour

Although both Snowy Owls and Great Grey Owls dependen on small mammals to breed, tehy differ strikingly in their hunting behaviour. While Great Grey Owls can visually detect small voles at least at 200 m distance (Nero 1980, Pettaway & Brunton 1969), they are more dependent on auditory cues to locate their prey (Höglund & Lansgren 1968). Great Grey Owls are well known for their ability to detect voles beneath 30-40 cm of snow, and plunge head-first with outstretched feet to grab their prey beneath loose snow (Nero 1980, Stefansson 1997). Even when voles are moving about under snow cover, Great Grey Owls can detect the sound of the moving prey at distances up to 50-70 m (Stefansson 1997). They usually perch in the lower third of grown trees, 4-6 m above ground (own observations). Great Grey Owls and Boreal Owls *Aegolius funereus* are the most extreme auditory hunters, and they both perch low when hunting voles (Norberg 1987). When hunting voles on fields and clear-cuts, Great Grey Owls often perch on fence poles and tree stumps. They have broad, rounded wings which give them a small wing load and good capacity for hovering. Often Great Grey owls will glide from a tree over a field or clear-cut, and hover before plunging down through snow or vegetation to grab its prey (Nero 1980, Stefansson 1997, own observations).

Snowy Owls are visual hunters, and they are able to see movement of small voles from more than 1 km distance (Solheim 2019a), and passerines the size of a European Starling from at least 1.6 km distance (Smith 1997). They usually perch on elevated landscape features like mounds, rocks or human made structures like pylons or fence poles, and scan the landscape for moving prey (Hagen 1952, own observations). In nesting areas in Norway, Snowy Owls select vantage points higher than their nests, with the highest vantage points as the most preferred hunting posts (Solheim et al. 2019). When a Snowy Owl spots a potential prey animal, it will take off and may fly more than 500 m before striking (Solheim 2019a). The wings of Snowy Owls are elongated, which gives them a higher flight speed than owls with more rounded wings (Cieslak 2017).

1.5 Hunting voles on tundra and taiga

1.5.1 Landscape constraints

Since Snowy Owls hunt in open landscapes like tundra, mountains and coast, steppe and prairie grasslands (Potapov & Sale 2012), visual detection of prey is probably a much better mode of hunting than by auditory cues. Heavy winds in such open landscapes would often make it impossible for an owl to hear the sound of moving lemmings and voles. Contrary it is usually much easier to hear movement of small mammals on the ground within a forest, where winds often calm down during evening and night-time. Hunting within a dense forest also strongly limits the distance for visually detecting moving prey. These differences between vast, treeless tundra and mountains versus taiga with dense forests may be the main factor explaining the different hunting techniques of Snowy and Great Grey Owls.

1.5.2 Fluctuating prey populations

A key feature of arctic and boreal ecosystems is a cyclic fluctuation of productivity of small mammals and gamebirds, with population peaks usually occurring every fourth year (Hagen 1952, Golley et al. 1975). These cyclic fluctuations are among the hallmarks of the biology of voles and lemmings, which are almost exclusively found in the Palearctic and Nearctic regions of the world (Wilson et al. 2017). Angerbjörn et al. (2001) analysed lemming cycle data from Fennoscandia during 137 years (1862-1998), and found that lemmings most often reach population peaks every fourth year, varying between 3 and 5 years. Lemmings peaked in southwestern Norway (the Hardanger mountain plateau) usually one year before the rest of Fennoscandia, where lemming population peaks were synchronised and almost exclusively happened within the same year (Angerbjörn et al. 2001). The cyclic fluctuations of small mammals also vary in amplitude, with increasing amplitudes at increasing latitudes and snow cover (Hansson & Henttonen 1985, Henttonen and Kaikusalo 1993).

Hagen (1952) described the role of the population cycles of lemmings and voles as the driving force for reproduction of owls, raptors and small carnivores. Owls and vole hunting raptors like Buzzards *Buteo* spp. and Kestrel *Falco tinnunculus* seem to turn up and nest successfully whenever voles reach a cyclic population high. This phenomenon is well known by ornithologists, wildlife enthusiasts, hunters and wildlife photographers alike, and was described already by Robert Collett in his chapter of lemmings (Collett 1912). Also typical generalist predators like Eagle Owls *Bubo bubo* and Golden Eagles *Aquila chrysaetos*, and even bird specialists like Gyrfalcons *Falco rusticolus* have their best reproductive years when voles and lemmings peak (Hagen 1952). Although these birds may all hunt lemmings and voles, larger prey like grouse, waders and hares also usually have good reproduction and large clutches the same year as voles reach their population peaks. When the rodent populations crash and almost seem to vanish, such alternative prey species are also diminished in numbers and reproductive output (Dahl 2005). The correlation between occurrence and reproduction of raptors and vole cycles were studied and documented by Yngvar Hagen, and inspired the alternative prey hypothesis (Hagen 1969, Angelstam et al. 1984). According to this hypothesis small mammal predators switch to hunting alternative prey species like grouse and hares when the microtine rodent populations crash. In light of this hypothesis Snowy Owls and Great Grey Owls are fundamentally different in their choice of prey. While Snowy Owls change from hunting lemmings and voles to mostly avian prey when vole populations crash or are shielded by snow cover (Campbell & MacColl 1978, Danilov et al. 1984, Smith 1997), Great Grey Owls go on searching for small mammals and avoid larger alternative prey (Höglund & Lansgren 1968, Mikkola 1983, Stefansson 1997, Kropacheva et al. 2019).

1.5.3 Theories of vole population fluctuations

The first written notes on fluctuating numbers of microtine rodents were made as early as in 1555 by Olaus Magnus, when lemmings where believed to fall from the sky during rainstorms and sudden rainfall (Magnus 1555; reprint in Swedish 1976). Collett (1878, 1895) published an extensive study on the lemming, describing the cyclic population outbreaks known as «lemming years». Collett could not find an explanation for these cycles, but he cited rural perceptions of lemmings eating themselves to death on fresh spring vegetation.

The population cycles of lemmings, voles and small game like grouse spp. and hares have puzzled biologists, hunters and wildlife scientists for more than a century. Many theories have been put forward to explain the forces driving such cycles. These can roughly be described as bottom-up versus top-down theories, where cycling species are controlled either by their food or by their predators. Contrary to these extrinsic factors, also intrinsic factors (behaviour, physiology, diseases) have been discussed as potential explanations for cyclic vole populations (Johnsen 2018). Angerbjörn et al. (2001) present the hypothesis of vole cycles: «*For a large number of species, it has been shown that dynamics co-vary across much larger regions than the scale of the local population (Ranta et al. 1997b, Koenig and Knops 1998, Koenig 1999, Bjørnstad et al. 1999 and references therein). This can be explained by either extensive dispersal (Ranta et al. 1997b), by the effect of nomadic predators, or by large-scale variation in resource availability or climate (the Moran effect; Moran 1953, Hudson and Cattadori 1999)*».

The top-down regulatory hypothesis have been intensively studied, especially linked to small game management and involving the alternative prey hypothesis (Hanski et al. 2001, Jahren 2017). Hanski et al. (2001) concluded that predation accounted well for the broad patterns in rodent oscillations found in Fennoscandia. A long term study on north eastern Greenland where four predators preyed upon Collared Lemmings *Dicrostonyx groenlandicus* as the only available microtine mammal, showed that all four predators played a key role at some point of the lemming cycle, but that only the Stoat *Mustela erminea* had the potential to drive the cycles by prolonging the low phase (Gilg et al. 2006). In a Finnish study Stoats and Weasels *M. erminea* were responsible for the main mortality of voles in the decline phase of oscillations (Norrdahl & Korpimäki 1995), and showed a time-lag in their numerical response to vole cycles (Sundell et al. 2013). Although this fulfils a condition for the specialist predation hypothesis stating that the predators drive the population cycles of their prey, it does not prove that mustelids actually are the driving force of vole population cycles. In a study in Poland, Zub et al. (2008) concluded that the negative impact of Weasels on their prey was limited in complex ecosystems in the temperate zone. In an experiment in England the removal of Weasels did not substantially alter the impact on vole survival or the cyclic dynamics of the experimental populations (Oli 2003).

The bottom-up hypothesis´ have usually dealt with nutrient content and amount of food plants (Norberg 1987). In Yukon Krebs et al. (2010) found that much of the variation in vole numbers could be explained by the indices of berry crops and mushrooms the previous summer, supporting a simple bottom-up hypothesis of population regulations. Selås et al. (2013) studied population fluctuations of plant-eating voles and moths, and found that the fluctuations could be caused by a positive effect of the supply of highly nutritious reproductive plant tissue. The one-year delay in population amplitude highs of the rodents however suggested that feeding deterrents in the plants were involved. The same conclusion could be drawn by the covariation of bank vole populations and moose calf weights linked to feeding deterrents in Bilberry

Vaccinium myrtillus, presented as the «mast depression» hypothesis (Selås 1997, Selås et al. 2001). Widen et al. (1987) also argued that fluctuations in plant food quality could partly explain the synchronous 3–4-year population cycles of voles and grouse in Scandinavia.

The driving forces of the cyclic population changes of voles and small game like grouse are still not fully understood, and most probably because the cycles are governed by a multitude of factors, as recently summed up by Oli (2019): «*Recent theoretical and empirical studies suggest that extrinsic factors (primarily food supply and predator abundance) may interact with population intrinsic processes (e.g. dispersal, social behaviour, stress response) to cause multiannual population fluctuations and to explain biological attributes of rodent population cycles*».

1.5.4 Are vole cycles levelling off?

Long-term monitoring on lemming and vole population cycles at Finse on the Hardanger mountain plateau showed that the cyclicity and size of peaks were closely linked to snow conditions, especially during spring (Kausrud et al. 2008). Although lemming peak years in this study were predicted to disappear after 1994, vole cycles at Finse have been regular with 3-4 years between population highs since late 1980ies, according to Norwegian terrestrial surveillance, but the size of the amplitudes have varied (Framstad 2019). In NE Greenland peak years of the Collared Lemming faded out during a long-term study fram 1995 (Gilg et al. 2009). In the boreal parts of Sweden, Hörnfeldt (2004) found a long-term decline in the populations of Grey-sided Voles *Clethrionomys rufocanus*, Bank Voles *C. glareolus* and Field Voles *Microtus agrestis*. The reduction in cycle high numbers was most extensively expressed in Grey-sided Voles with declines since the 1970s, followed by Field Voles which declined from the 1980s. The least reductions were found for Bank Voles, but also this species showed reduction, especially with respect to spring densities. According to Hörnfeldt (2004) the reductions were largely caused by stronger declines during winter. Grey-sided Voles also declined in Finland (Hansen et al. 1999, Henttonen 2000), but the declining cycle amplitudes were recorded at later years than in northern Sweden (Hörnfeldt 2004). In southern Finland the vole cycles temporarily disappeared in the latter half of the 1990s, but returned to former strength after about five years (Brommer et al. 2010).

Cornulier et al. (2013) compiled cycle data on voles covering at least 18 years, from across Europe, and concluded that especially *Microtus* Voles and Grey-sided Voles with a few exceptions had undergone cycle declines, with low amplitudes around 1995-2005. Several studies have however shown that the amplitudes, and especially the *Microtus* voles, have returned since the early to mid-2000s. In a study in northern Finland 2006-2010, Field Voles returned with increasing populations in autumn 2010 (Savola et al. 2013). Wegge and Rolstad (2018) monitored small mammals in a boreal forest study area in southern Hedmark during a 39 year period (1979-2017). They found that all species of microtine voles fell markedly in numbers during the 1990s. The reduction was most distinctive in clear-cuts, where the Field Vole almost vanished completely. From the late 2000s, the abundances of all species recovered to the levels seen before 1990 and beyond (Wegge & Rolstad 2018). Erich et al. (2019) concluded that there was no consistent declining trend for lemming species around the Holarctic, but negative trends were detected in some low arctic populations where lemmings co-occur with one or more vole species.

The lemming situation in Norwegian Snowy Owl nesting habitats has been followed since the Norwegian Snowy Owl Project was started in 2005 (Jacobsen et al. 2018). Lemmings peaked in Northern Norway and made nesting possible for Snowy Owls in 2007, 2011 and 2015. Although especially *Microtus* voles clearly went through a period almost without typical cycles and peak years during a 10 year period from 1990 to 2000 (Wegge & Rolstad 2018), they seem to have regained their former cyclicity during the last three cycles, reaching peaks in Hedmark in 2011, 2014 and 2018 (paper VI). It is thus an open question whether vole cycles in Fennoscandia have levelled off, or just temporarily gone through a long-term dip with low populations and missing peak years.

1.6 Owls, voles and climate

The world´s climate is changing, and mean temperatures seem to increase most in high latitudes (Thuiller 2007, Allen et al. 2018). In Fennoscandia these changes are expected to cause more changes in weather, with increasing temperatures and precipitation (Stenseth et al. 2003, Hansen-Bauer et al. 2008). Weather is changing in all ecosystems on the planet, and is a major threat to the planet´s biodiversity (Thuiller 2007, Pimm 2018).

Birds may move to new wintering locations, following changes in advance and severity of winters (Pávon-Jordán 2017). Both resident and migratory birds change their summer distributions due to milder climate, moving north (Elmhagen et al. 2015). Changes in phenology at the breeding sites of migratory birds may create a mismatch with their food resources, resulting in reduced reproductive output, even though the birds may manage to change their time of migration (Saalfeld et al. 2019).

Wegge and Rolstad (2017) found that warmer springs enhanced breeding success in forest grouse, contrary to predictions that warmer summers may reduce the reproductive output for these birds (Selås et al. 2011). Changes in temperature and snow cover, and the start of spring thawing have effects on Bilberry (Selås et al. 2015), which is a crucial food plant for both rodents, grouse and moose in the boreal forest (Selås et al. 2001). Snow cover has fundamental impacts on hunting behaviour and migration strategies of owls and vole-eating raptors (Sonerud 1986), sheltering voles and changing their availability for different vole hunters. In a 12 year study in Finland, autumn rainfall increased while the number of days with frost decreased, both influencing the availability of Bank voles and days for food storing by Pygmy Owls *Glaucidium passerinum* (Terraube et al. 2016). Although the climatic changes have been demonstrated globally, effects on small mammals like voles and mustelids remain uncertain, and still subject to discussions, new hypotheses and predictions (Ylönen et al. 2019). The return of vole cycles after 2010 has also been held as an argument that climatic changes is not responsible for the dampened vole cycle amplitudes which were reported in Fennoscandia in the 1970s and 1980s (Brommer et al. 2010).

Changes in winter duration, precipitation, snow cover, and cyclicity and amplitudes of microtine rodents may have profound effects on vole hunters like Snowy Owls (Jacobsen et al. 2014) and Great Grey Owls (Hipkiss et al. 2008). Heavy summer rainstorms may kill Snowy Owl chicks not shaded by the female (Jacobsen et al. 2014), and climate change may increase the risk of mosquito or blackfly attacks on chicks and adults and ruin clutches (Solheim et al. 2013). Shorter winters with rainfall on snow and less snow cover may also lead to collapsing lemming populations before spring thaw, thus preventing Snowy Owls from initiating breeding (Jacobsen et al. 2014). The collapse of the cycles of collared lemmings in eastern Greenland has had dramatic effects for Snowy Owls which formerly bred regularly in this part of the Arctic (Schmidt et al. 2012). Snowy Owls hunt seabirds and marine ducks in open water in the drift ice during winter (Robertson & Gilchrist 2003), and milder climate could lead to larger patches of open water and reduced hunting success of Snowy Owls (Therrien et al. 2008; 2011). Reduced amplitudes of vole cycle peak years result in smaller clutch sizes for Great Grey Owls (Hipkiss et al. 2008).

Milder winters with rainfall could create more hard crust snow, preventing Great Grey Owls from plunge-dive hunting (Nero 1980) through the snow. The breeding performance of vole-eating boreal owls is directly affected by climate to a much larger extent than formerly thought, according to Lehikoinen et al. (2011). Although reduced length of snow cover is expected to increase the amount of voles hunted by avian vole predators, understanding the full implications of milder climate and changed snow regimes on food webs and ecosystems is a complicated field to study (Penzykowski et al. 2017). Although small mammals are monitored through the Norwegian national TOV program (Framstad 2019), surveillance of species dependant on these prey animals will also likely reveal changes in cyclicity and cycle amplitudes. It is thus paramount to monitor the population development of vole hunters of both threatened and expanding species in a changing climate.

2. Monitoring Snowy Owls and Great Grey Owls

2.1 Searching for nests and nest sites

Monitoring wild animals demands surveilling a species' population size (i.e. counting number of individuals), reproduction and distribution. An understanding of factors limiting bird populaions is crucial for management (Newton 1998), especially of threatened species. Monitoring threatened birds is part of the Norwegian national surveillance program TOV (Framstad 2019). Since recommendations in 2010 (Ims et al. 2010) this monitoring has also been focused on effects of climatic change.

Knowing the size of populations is a basic prerequisite for wildlife management, whether dealing with game (Storaas & Punsvik 1996), or threatened raptors (Meyburg & Chancellor 1994). Individuals can be counted in the wild, as is widely done when surveilling ungulate herds from plane or helicopter. Birds can be more difficult to count, either because they are difficult to observe or nest in remote, inaccessible areas.

Great Grey Owls most often nest in Goshawk A*ccipiter gentilis* or Common Buzzard *Buteo buteo* twig nests, which usually are built within mature coniferous forests (Stefansson 1997, Berg et al. 2011). Finding such twig nests is both laborious and time demanding. Many Great Grey Owls were found nesting in Hedmark in 2011 only because nests of the two raptor species had been monitored for several years (Berg et al. 2011). Artificial nests and nesting platforms have later become more common as nesting places for Great Grey Owls (Berg et al. 2019). Although the percentage of nests found on such platforms has increased, this cannot explain the original expansion and establishment of the first nesting Great Grey Owls in Hedmark in 2009-2011 (Paper VI). Snowy Owls are difficult to count because the majority of the world´s population nest in remote, inaccessible areas on tundra in Russia, Canada and Alaska (Portenko 1972, Cramp 1985). Surveying Snowy Owls in Fennoscandia is both expensive and time-consuming (Øien et al. 2016). The fact that they only start nesting in an area where lemmings and voles have a population peak, means that nesting owls in a given area at best only can be surveyed each fourth year. Clutch size can be surveyed in June when the owls have eggs, but if the lemmings and voles crash early in summer, clutches with chicks and eggs may later be abandoned totally (Øien et al. 2016). Counting the number and frequency of juvenile and young Snowy Owls during autumn and winter following a summer of breeding opportunities may thus present a better picture of the reproductive success of Snowy Owls.

2.2 Surveilling age structure

Knowing the age structure of a population is vital, since mortality and reproduction usually varies with age. The age at which an individual starts reproduction has direct influence for the individual´s fitness and lifetime reproduction (Brommer et al. 2002). The age at which Tawny Owls *Strix aluco* start breeding have direct impact on the number of life-time recruits for each individual (Millon et al. 2010). The same has been documented for Ural Owls *Strix uralensis* (Brommer et al. 1998). In both Tawny Owls and Ural Owls the vole cycle phase for first time breeders had the strongest effect on lifetime reproductive success (Brommer et al. 1998, Millon et al. 2010). Female Tawny Owls which postponed reproduction to breed for the first time as 3 years old during an increase phase produced more recruits to the population, but for males no such effects were detected (Millon et al. 2010). Knowing the age of the breeding birds is thus fundamental when studying population reproduction and recruitment. For the endangered Lesser White-Fronted Goose *Anser erythropus* increasing adult survival has been the key management measure to save the remnant population in Fennoscandia (Jones et al. 2008), demonstrating the importance of knowledge of age structure in bird populations.

3. Moult, plumage and age

Moult patterns and the wear of feathers is essential knowledge when aging birds (Svensson 1992, Jenni & Winkler 1994 Pyle et al. 2008). Many birds display different plumages for immatures and adults. Based on such plumage characters, most raptors can be aged accordingly (Forsman 1984, 2016). White-tailed Sea Eagles *Haliaeetus albicilla* reach their mature plumage after five years, and mapping the successive plumage characters is a time-consuming effort (Helander et al. 1989). Golden Eagles use at least six years to reach adult plumage (Tjärnberg 1988), but have more easily recognisable differences in wing feathers as they age than have White-tailed Sea Eagles. Moult of both body and flight feathers are clues used by bird ringers to age passerines (Svensson 1992, Jenni & Winkler1994) and waders (Prater et al. 1977, Message & Taylor 2005). Most ducks, geese and swans *Anatidae* spp. and cranes *Grus* spp. moult all their flight feathers simultaneously, and remain flightless until the next generation of feathers are fully grown (del Hoyo et al. 1999). Raptors and owls cannot adopt such moult strategies for obvious reasons, as they cannot hunt without being able to fly. For large raptors it takes 40-60 days for a flight feather to regrow after moult (Edelstam 1984), and in the Eagle Owl 56-84 days (Penteriani & del Mar Delgado 2019). These birds thus moult flight feathers in a serial sequence, leaving only small gaps in their wings at any time during moult. Edelstam (1984) described moult sequences of large raptors by studying skinned birds in museum collections. He used the state of wear and bleaching (fading) of feathers to reconstruct the details of underlying moult processes. Such moult patterns are of paramount importance in the development of surveys in which age is a key parameter (Zuberogoitia et al. 2013).

4. Objectives

My objective for this study was to develop methods for aging and identification of individual Snowy and Great Grey Owls without the need to trap the birds, and to implement the methods in studies of free ranging owls of both species. The first step was to study the moult sequences of Great Grey Owls and Snowy Owls and how the patterns of wing feathers of different age can be used to age both captured and free-ranging owls (paper I & II). Based on differences in bar patterns of wing feathers I developed a method for identifying individuals of the two owl species by comparing wing images of both captured and free flying birds (paper III). I applied these methods and used both moult sequences and wing bar patterns to study the age structure of both Snowy Owls (paper IV) and Great Grey Owls (paper V). Finally I demonstrate that these methods can be used on observations collected through public sciences, as during irruptive appearances of Great Grey Owls (paper VI).

5. Material and methods

5.1 Terminology and numbering of feathers

Bird feathers have been given different names according to which part of the body they cover. In this study I focus on the flight feathers (paper I and II), and to a lesser extent to tail feathers (paper VI), because it takes 3-4 years for large raptors to renew all their flight feathers while all tail feathers are often moulted each year (Gura et al. 2017). The large wing feathers and tail feathers are often termed remiges and rectrices (del Hoyo 1992). Here I use the popular terms *wing feathers* and *tail feathers*. Wing feathers are separated in primaries attached to the hand, secondaries attached to the ulna and tertiaries attached to the innermost tip of the ulna (Fig 1). Tertiaries are in a strict sense also secondaries, but have been given a different term because they are shorter than the rest of the secondaries. While most authors treat them separately from the longer secondaries, some (Cieslak 2017) count them as secondaries. I have not included the tertiaries in the initial moult descriptions of Great Grey and Snowy Owls (paper I and II), because they are often omitted in moult descriptions (Mikkola & Lamminmäki 2014).

Most birds have 11 primaries, but the outermost primary is usually rudimentary or missing (del Hoyo 1992), as in owls (Cieslak 2017). The number of secondaries vary from only 6 in hummingbirds to 32 in some albatrosses (del Hoyo 1992). Many birds have 11 secondaries, which is common for most of the owls as well. Species of the genus *Bubo* represent an exception, with 14 to 16 secondaries (Solheim 2011, paper II). While flight feathers in passerines are numbered inwards, starting with the outermost primary as P1 (Svensson 1992), I have used the numbering proposed by Stresemann & Stresemann (1966) which is usually adopted for raptors (Forsman 1984) and owls (Cieslak 2017). Primaries are thus numbered starting from the carpal joint (P1) and ending with P10 as the outermost primary. Secondaries are numbered inwards from the carpal joint, with S1 as the outermost secondary, adjacent to P1, and with S11 (Great Grey Owls) or S15-16 (Snowy Owls) as the innermost secondary adjacent to the tertials (Fig 1). In Snowy Owls P7 is the longest primary, the tip often protruding and exposed on a perching bird (Fig 2). On Great Grey Owls the primary P5 is the longest primary.

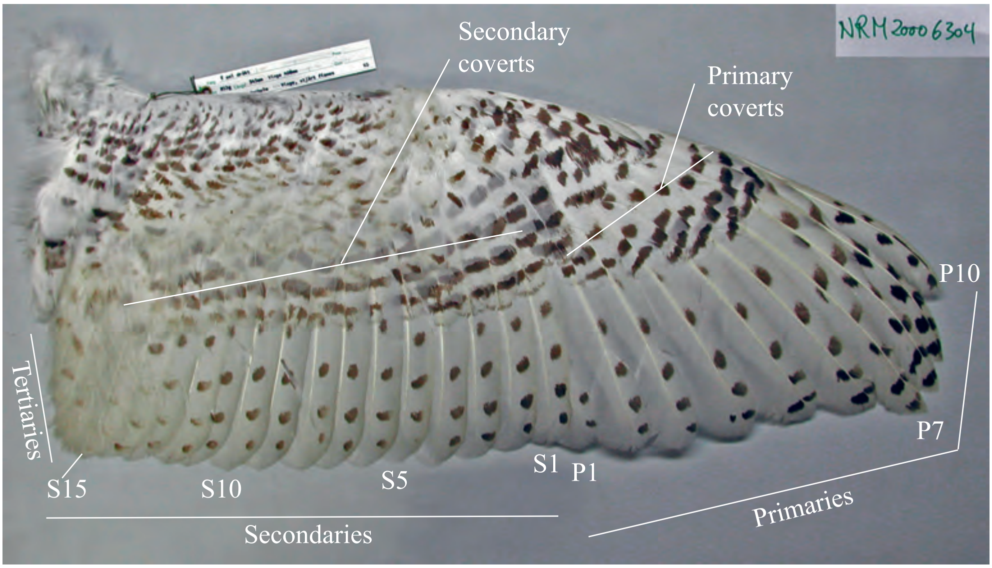

Figure 1 Wing of a young male Snowy Owl found dead July 3, 2000 in northern Sweden before start of the first moult, showing numbering of primaries and secondaries. Note also the gradually increasing wear and bleaching of dark bars on outer vanes of secondaries towards the tertiaries.

Figure 2 Female Snowy Owl perched on a fence pole in Saskatchewan, Canada, February 17, 2016. Note protruding tips of the longest primaries (arrows).

The shaft or quill of a feather is also known as the rachis. On both sides of the rachis are the vanes. Flight feathers typically have an outer and an inner vane, where the inner vane is wider than the outer vane. The vanes do not extend to the start of the rachis, leaving the innermost part of the quill as a round, stiff tube. The innermost part of the flight feathers is covered by smaller feathers, called coverts. Those on top of the primaries are primary coverts, while the ones covering the secondaries are called secondary coverts. These coverts are also moulted, and often together with the corresponding flight feather. This corresponding moult is most easily and often seen with primary coverts and underlying flight feathers.

5.2 Terminology of age and moult

I have used the ageing categories for birds proposed by Runde (1991). A bird is said to be in its first calendar year (1CY) from the time of hatching until 31 December. In the following year it is 2CY, and so on. A bird of unknown age, but at least in its X calendar year, is termed XCY+. I have added the suffixes “a” (autumn) for birds found in July-December, and “s” (spring) for birds found in January-June. During summer of their second year of life (2CY), owls moult their first flight feathers, and this moult is termed M1. Next year they enter M2, and so forth.

5.3 Wear and bleaching of feathers

Bird feathers are subject to mechanical wear as they age, and the degree of wear indicate the age of singular feathers (Edelstam 1984, Forsman 1984). Turbulence around the wing of a flying bird puts extra stress on flight feathers causing feathers to vibrate. In addition to the gradual wear caused by flying, preening and rubbing against other feathers and vegetation, bird feathers are also bleached by sunlight (Newton 2009). The degree of bleaching varies with habitat and the intensity of sunlight. Birds which spend much of their time shielded by vegetation are thus subject to less direct sunlight than birds perching unshielded in open landscapes. Different feathers are also subject to differences in sun exposure (Figs 1 and 2). Great Grey Owls and Snowy Owls spend most of their time perching, even when they are actively hunting. Most of the wing feathers are hidden on a perching bird. The most exposed feathers are the tips of the longest primaries, and the outer vane of the innermost secondaries and tertiaries close to the back of the bird (Fig 2). On a juvenile bird where all flight feathers are of the same age, these feathers are more heavily worn and bleached than the rest of the flight feathers before the first wing feather moult starts. On one year old juvenile Snowy Owls secondaries are gradually more worn and bleached from the first to the innermost secondary (Fig 1).

The colouration of feathers of Great Grey and Snowy Owls is caused by the pigment melanin (Cieslak 2017). White feathers or parts of feathers are colourless because a lack of melanin. Dark feathers with melanin are harder and stronger, and resist wear better than light feathers (Bonser 1995). On feathers with dark and light bars the light patches wears off faster than the dark patches (Cieslak 2017). This difference in resistance may create a serrated edge on the outer vane of barred wing feathers as they age, helping to judge the age of a singular feather in an owl´s wing.

The northern latitudes of the tundra and taiga zones offer vast differences in sunlight exposure through the year. While the sun stays below the horizon north of the polar circle during winter, it shines continually during summer. On northern tundra and at high elevations in Fennoscandia, snow cover may not start to melt before late May or early June. Snowy owls are thus exposed to intense sunlight during the start of the breeding season, and the strength of this sun exposure is enhanced by the snow albedo. The plumage of a Snowy Owl is thus subject to increasingly intense sun bleaching from March to June. Great Grey Owls usually hunt within the boreal forests, shaded by trees, and are thus subject to much less sun exposure and bleaching than Snowy Owls. When voles crash the owls may however move outside the breeding areas into open fields to hunt (Solheim 2014), and may then be subjected to more sunlight than when hunting in the breeding area forests.

5.4 Differences between juvenile and adult feathers

In general, juvenile flight feathers of owls have narrower dark bars than later, adult flight feathers (Pyle 1997), especially the terminal dark bar. They also often have more pointed tips. Pyle (1997) described moult of North American owls, but did not provide photos to show how such differences may look like. While it may be difficult to see if a single flight feather is juvenile or adult, it is usually easier to become aware of the differences when both generations are present in an owl wing.

In Great Grey Owls the juvenile flight feathers have narrow, irregular outer dark bands (paper I). The next generation of flight feathers are strikingly different, with a broad, outer dark band. The distance from the outermost dark band to the tip of the feather is usually broader than the broadness of the terminal dark band. These differences are easily seen on a wing of a Great Grey Owl which has moulted once (Fig 3). For Great Grey Owls there is also a distinct difference between juvenile and adult tail feathers, a difference which makes it possible to separate young from older Great Grey Owls based on photos of perching birds (paper VI).

Snowy Owls are more challenging to age, because they are sexually dimorphic. It is much easier to see the difference between juvenile and adult feathers in females than in males. While females usually retain dark spots or bars on all their flight feathers as they age (Fig 4), males usually lose all or most dark markings in their wings as they age (Fig 5). Heavy mottling is a distinct character of juvenile feathers, but the degree of mottling is highly variable (Fig 6). Mottling is often found on the primary and secondary coverts of juveniles. During spring bleaching, these markings may totally vanish.

Figure 3 Wing of a female Great Grey Owl which has moulted once. Note the difference in width of outer dark bars on juvenile (J) and adult feathers. Photo: Trond Berg.

Juvenile flight feathers of both female and male Snowy Owls are slightly narrower with more pointed tips than adult feathers. Like in Great Grey Owls, they also usually have irregular and narrow terminal, dark bars, best expressed in females. On females the dark bars on primaries stretches across the inner vane. On adult primaries dark bars are shorter, usually covering less than half the width of the inner vane, or only covering the outer vane. The distance between bars is also longer than on juvenile primaries (Fig 7). Juvenile secondaries of females have four or five visible dark bars on the outer vane. On the next generation there are only three visible bars. On males the dark markings on juvenile feathers are smaller and more like dark spots. There are usually not more than three such spots visible on the outer vane of juvenile secondaries, creating an even band of markings (Fig 4). Some juvenile males may however have irregular number of such spots on the secondaries (Fig 6). Secondaries of adult males are usually without such dark spots (Fig 5). Primaries of juvenile males have shorter dark bars or smaller spots than females, but usually show irregular terminal bars like females, often with mottling (Fig 5 and 6). The next generation of primaries have longer distance from the terminal dark bars/spots to the tip of the feathers, and fewer markings than on the former juvenile primaries (Fig 8).

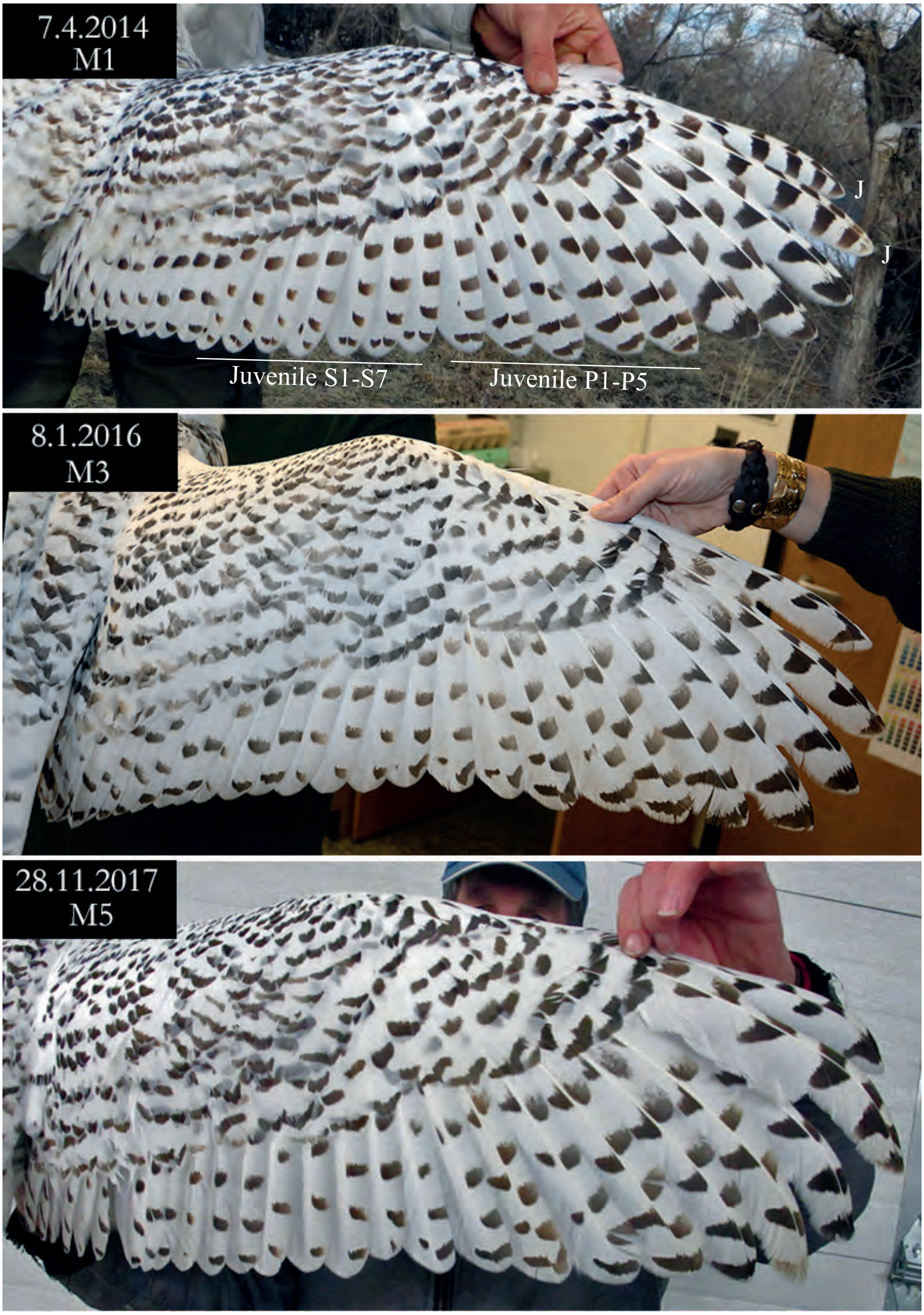

Figure 4 Wing images of the same female Snowy Owl after one, three and five moults. Juvenile feathers are only present in the upper image, after M1. Photos: Dan Zazelenchuk.

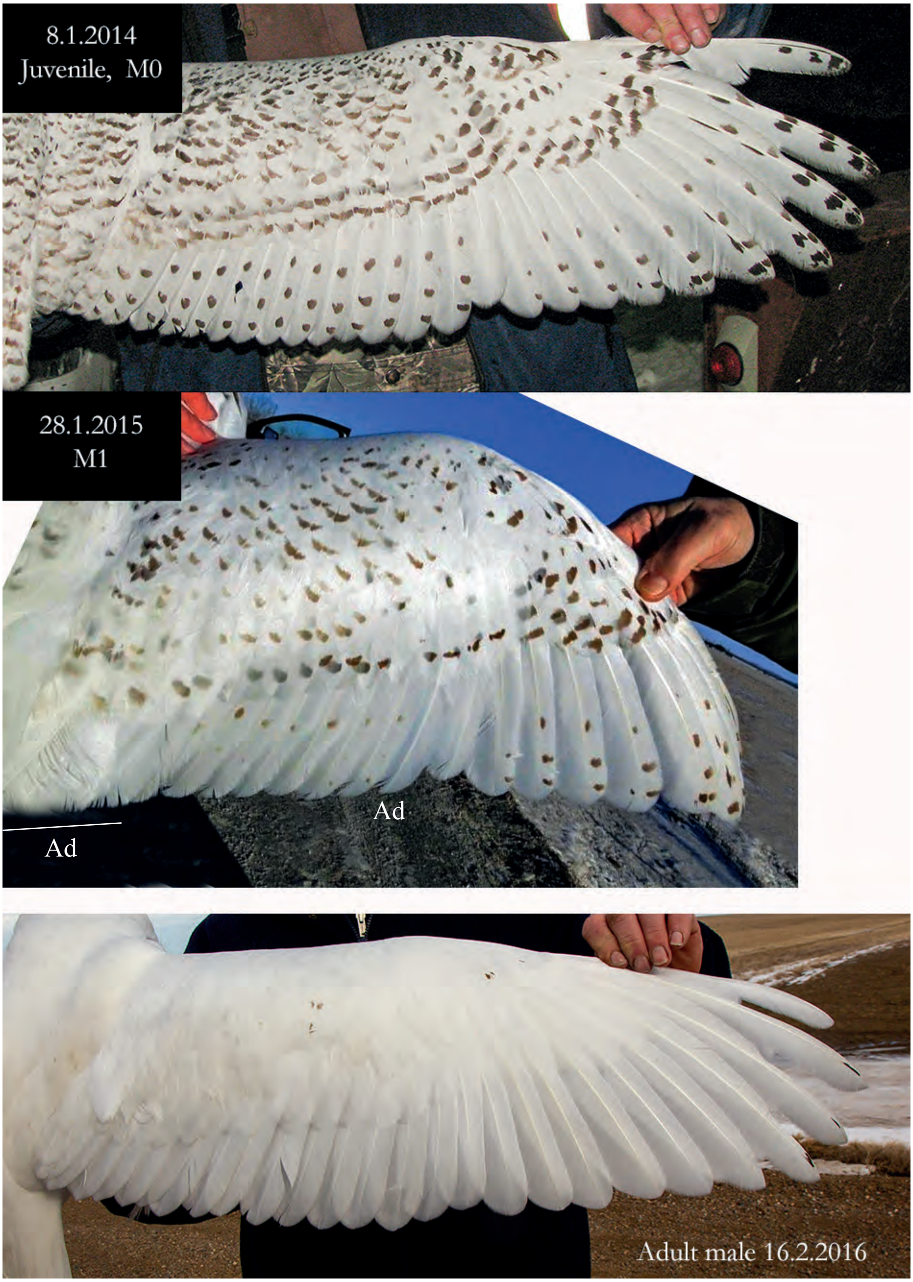

Figure 5 Wing images of a male Snowy Owl before and after the first moult M1, showing bleaching of dark spots on wing feathers. Note that many of the dark spots on secondaries have totally vanished by bleaching after one year. Only S2 and S10-15 are new (Ad). Wing of an adult male for comparison. Upper two photos: Tom McDonald.

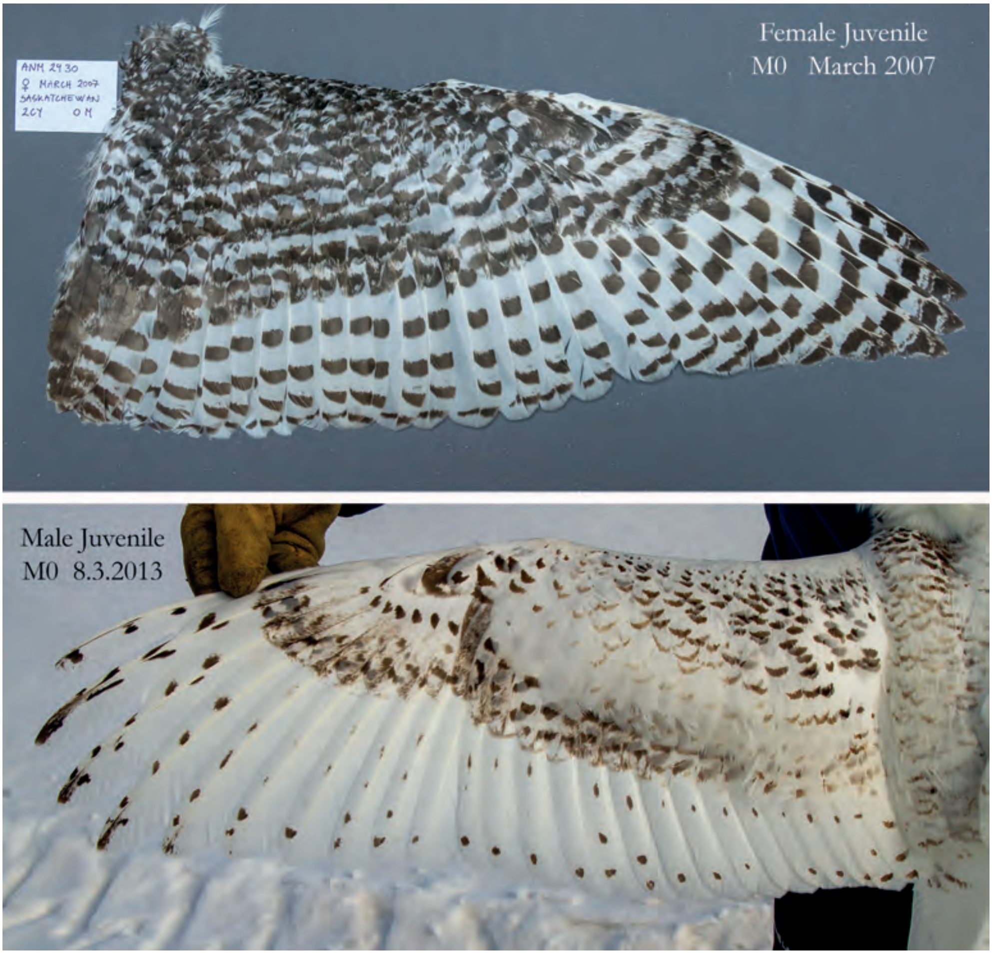

Figure 6 Wings of juvenile female and male Snowy Owls before the first wing feather moult, showing mottling on coverts and outer tips of primaries.

5.5 Sampling wing images

Any protocol for capturing owls for banding or other studies should include taking photos of the outstretched wings. It is usually most convenient to do this when two persons work together. While one holds the owl, the other can concentrate on taking good wing images (paper III). It is paramount that the feathers are arranged so all outer vanes are visible, and that feathers are not ruffed up. Feathers can easily be smoothed by stroking them through one´s fingers, in the same fashion as a bird does using its beak when preening. The wing must

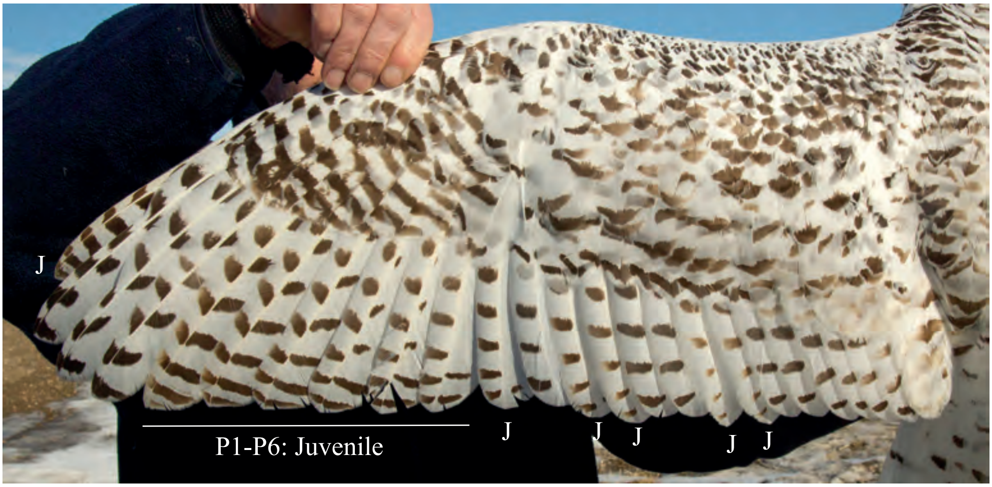

Figure 7 Wing of female Snowy Owl after first moult M1, showing difference between juvenile and adult wing feathers.

Figure 8 Wing of male Snowy Owl after first moult M1, showing difference between adult primary P7 and juvenile primaries. Note bleaching and wear of juvenile secondaries. Photo: Tom McDonald.

be totally stretched so all primaries are visible. The outermost primary P10 is easily covered by the next P9, so holding the wing correctly is vital. P10 is often not moulted until third or fourth moult, and it may be crucial when judging moult stage if this feather is still juvenile or has been moulted.

It may not be as easy to take proper wing images for a person working alone. The problem can be solved by using a camera on a tripod and time-delayed triggering (paper III). The best cameras to use are compact cameras with a flexible viewer screen which allows the person holding the owl to see how the wing aligns up with the camera view. This allows adjusting ones position so the whole wing is covered before the camera shutter is triggered. This method has been used with great success by my co-workers in Canada and USA.

While a bird in hand is easily positioned to get optimal wing images, this is not an option when encountering free flying birds. In the wild one has to deal with how the situation and opportunities are presented (paper III). Modern digital system cameras can take 6-14 images per second, and thus capture flight sequences where at least some images may show upper and under sides of both wings. The best images to use for both moult studies and individual identifications are images showing the upper side of a flying owl´s wing (Fig 9). However, underside images can also be used (paper III). When comparing an underside image with an upper side image for identifications, one of the images should be inversed to ease comparison of bars and patterns (paper III).

5.6 Comparing bar patterns on wing images

The dark bars on vanes can vary in many characters. Bars are compared with respect to the length and width of a bar, distance between bars, how bars on outer and inner vanes are aligned, and the shape of the edge of each bar. When bars on several feathers can be compared, they together usually form a unique pattern which can be recognised even on images of medium quality (paper III; Fig 7). Patterns of dark bars and spots can also be used from other parts of the body, depending on which parts of the body are available for comparisons on an image (Fig 10, paper IV: Fig 4). Differences in one bar pattern are sufficient to conclude that two wing images portray different individuals (paper III: Fig 11).

When comparing wing images from different years, I select the newest, most recently moulted primaries on the oldest image. The number of summer periods which have passed before the next image is taken defines the number of moults between the two images. On the newest image I look for age and wear of the primaries at the same places as the fresh ones in the oldest image. Based on the moult cycles (paper I and II) it is possible to judge whether these

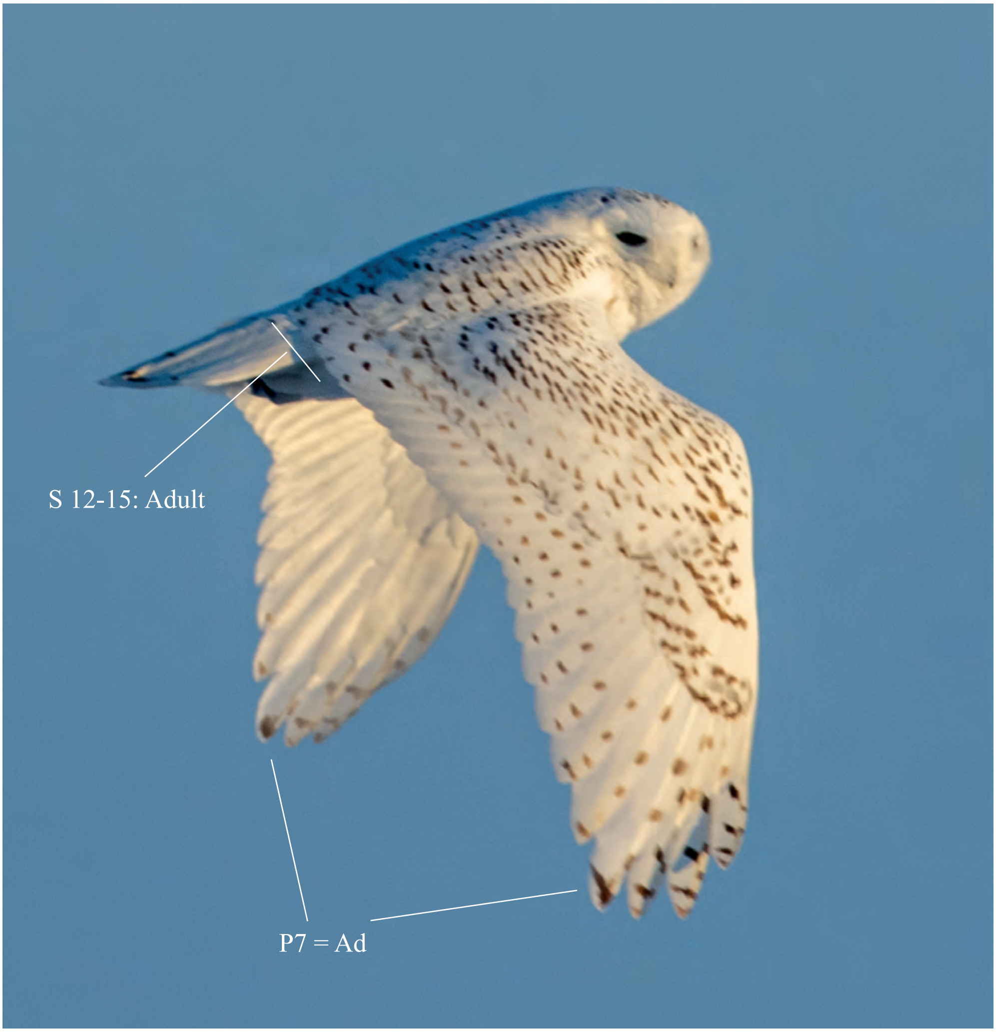

Figure 9 A male Snowy Owl photographed in flight February 13, 2016 in Saskatchewan, Canada. Juvenile and adult wing feathers can be separated on images like this one. The bird has moulted once, and is thus a 3CY bird.

primaries should still be unmoulted or fresh on the newest image. If they are expected to be unmoulted from the old to the new image, bar patterns should also be expected to be identical if the images portray the same owl individual, or different if they portray different individuals. Such comparisons is most easily done on retained juvenile feathers, since they obviously cannot have been moulted.

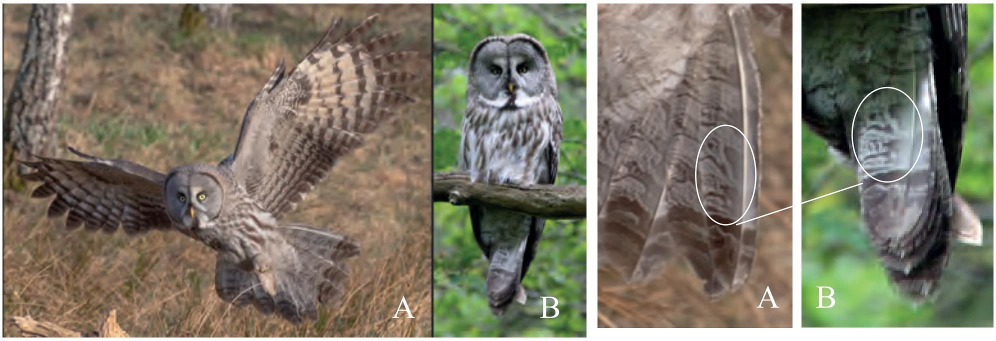

Figure 10 Great Grey Owl photographed March 28, 2019, west of Mandal (A) and 7.5km further west June 7, 2019 (B; photo: Inger Stray). The photos allow comparing of bar patterns on the outermost left tail feather, revealing that the images portray the same individual. The owl is unbanded, so feather identity functions as individual marking.

5.7 Sample sizes

5.7.1 Great Grey Owl

The moult studies started with examining museum skins of Great Grey Owls. At the Natural History Museum (NRM) in Stockholm, Sweden, 58 Great Grey Owl skins of birds which had been banded as nestlings, were examined (paper I). The 58 skins included 8 juveniles, 12 birds in moult stage M1, 11 in stage M2 and 27 older individuals. The collection did not include any owls in moult stage M3.

The moult study of the Great Grey Owl was conducted at the very start of the expansion of the species as a regular breeder in Hedmark county in SE Norway from 2009. Outstretched wings of a majority of the adult breeders which were captured for banding purposes were thus photographed according to protocol since 2010. Photographs were also taken of flying adults which could not be captured. Since 2011 wing images have been sampled from 224 adult nesting birds, the majority provided by Trond Berg. A total of 48 breeding birds had formerly been banded, of which 15 had been banded as nestlings and 17 as young adults of known age according to their moult patterns. The last 16 had lost all juvenile wing feathers at time of first control and could not be aged more exactly than as 5CY+ (paper V).

5.7.2 Snowy Owl

The moult studies of Snowy Owls originally started as part of a project to collect DNA samples from museum skins in the Nordic countries (Solheim et al. 2004). Almost 400 skins were photographed, but no attempts were made to separate wing feathers for closer study

Figure 11   Almost 400 Snowy Owl skins were photographed from all sides during the first skin study conducted in 2003-2004 (Solheim et al. 2014). Natural History Museum, Stockholm February 3, 2004. Photo:Gunnhild Marthinsen.

(Fig 11). The visit to NRM in January 2010 revealed that the museum also held a large collection of Eagle Owl skins of known age. The museum was thus visited again in August 2010, and wings of 32 Eagle Owls of known age were photographed for moult studies (Solheim 2011). The moult of this species was studied as a blueprint to interpret patterns found in the closely related Snowy Owl, since no museum collections to my knowledge hold skin samples of Snowy Owls which have been banded as nestlings and recovered after their first wing feather moult (paper II). I examined a total of 378 Snowy Owl skins, and selected 53 which clearly had some juvenile wing feathers, for closer examination. The 53 skins included 20 birds in moult stage M1, 19 in moult stage M2 and 10 in moult stage M3. Snowy Owl skins were checked in the collections of the Natural History Museum of Stockholm (NRM), the Zoological Museum of Oslo (ZMO), the Zoological Museum of Copenhagen (KZM) and the Smithsonian Institution, Washington (SMS). A specimen from the Zoological Museum, Helsinki (HZM) was also included.

Since 2010, the Norwegian Snowy Owl Project has cooperated with Canadian Snowy Owl banders (Solheim et al. 2014), and they have provided a large sample of wing photos from captured Snowy Owls. Many photos have also been provided from New York State, USA. Since 2013, I have received wing photos of 186 captured Snowy Owls from Tom McDonald (New York; 119), Dan Zazelenchuk (Saskatchewan, Canada; 36), Mike Blom (Alberta, Canada; 26), and Marten Stoffel (Saskatchewan; 5). Since 2010 I have visited Saskatchewan and Alberta 7 times, gathering many photos of free-flying Snowy Owls. These photos of free flying owls have not yet been subjected to moult and ID analyses.

6. Results and discussion

6.1 Moult (paper I and II)

Although moult sequences can be studied and interpreted from museum bird skins alone (Edelstam 1984), access to individuals of known age are essential to control the validity of such interpretations. Birds which have been banded as nestlings provide such opportunities if they are later recovered dead or recaptured. From 1955-2012 a total of 3073 Great Grey Owls were banded in Sweden (Solheim & Stefansson 2016). Of a total of 1358 Great Grey Owls banded between 1997 and 2012, 1083 were banded as nestlings. In Sweden, most owls and birds of prey are defined as «Crown´s game», and dead specimens must be delivered for research purposes (Edelstam & Delin 1975). This has ensured that the national Natural History Museum (NRM) for many years has been able to make substantial collections of skins from owls and raptors, containing many birds with known age. The museum protocol of making skins with one loose, outstretched wing also enhance the possibilities for moult studies. All wings could thus be photographed and subject to later analyses. The material on Great Grey Owls gave a good coverage of the first two moult stages, but could not reveal how Great Grey Owl wings should look like after the third moult.

The expanding population of Great Grey Owls in Hedmark county, Norway, has been followed and studied closely since 2009 (Berg et al. 2019), with 543 nestlings and 155 adult nesting birds banded (paper V). A total of 48 formerly banded nesting birds were controlled, of which 15 had been banded as nestlings and 14 when they were in the age categories 2CY-4CY (i.e. with known moult patters M0-M2 as described in paper I). Wing photos have thus been

Tab 1. Information on moult stage M3 from controls of banded adult Great Grey Owls.
*: Owls which had not been formerly banded, but where age was interpreted from the moult pattern.

Band no	contr year	Sex	Age when banded	Year	Juvenile feathers
234643	2014	F	2CY	2011	0
232673	2014	F	pull	2010	P1 (LW) 0 (RW)
237697	2017	F	pull	2013	0 (both w)
232085	2018	F	pull	2014	0
232869	2018	M	pull	2014	0
234219	2018	F	4CY	2017	P1, P2 (both w)
232677	2018	F	pull	2014	0
232646	2014	F	*	-	0 (LW) P1 (RW)
232679	2014	M	*	-	P2 (both w)
231284	2017	F	*	-	P1 (LW)
232747	2018	F	*	-	P1 (both w)

gathered from 7 individuals in the 5CY category and 4 individuals showing moult patterns interpreted to be in the same category (Tab 1). While five of these individuals had retained one juvenile primary, one had retained two in both wings. These were either P1 or P2. Another important feature of the third moult M3 is that some innermost secondaries and the tertiaries have been moulted for the second time. They thus stand out as more fresh and darker than the adjacent secondaries. Since moult M1 always involves the innermost few secondaries and tertiaries, and are followed by secondaries further out during M2, the innermost secondaries must have been moulted for the second time when they appear more fresh than the following adult secondaries (see also Snowy Owl). Fresh inner secondaries and at least one retained juvenile primary should thus be sufficient to classify a bird as 4CYa (autumn) or 5CYs (spring).

The first attempts to age Snowy Owls based on body plumage was not successful (Solheim et al. 2004), and the photos of nearly 400 Snowy Owl skins were left for later analyses. The Snowy Owl was recently reclassified as a *Bubo* species (Banks et al. 2003), based on DNA analyses and close relations with the Great Horned Owl of North America. I thus found it plausible that the Snowy Owls could moult in a similar sequence as other northern *Bubo* species, and chose the Eurasian Eagle Owl as a reference.

Figure 12 The majority of Snowy Owl skins in the world´s museums have wings closed to the body. Wing feathers must be carefully bent out to check for age and wear. Smithsonian Museum, Washington, February 22, 2011. Photo: David Johnson.

The moult of Snowy Owls was challenging to study, primarily because no Snowy Owl skins existed of birds which had been banded as nestlings, but also because most of the Snowy Owl skins studied were old and made with closed wings (Fig 12). The difference in number of dark bars/spots on outer vanes of juvenile and adult secondaries was thus first noted when outstretched wings of captured birds could be studied (see caption 5.4). It is challenging to keep trace of differences of 15-16 secondaries when one feather at a time must be carefully bent out from a folded wing to study wear and age. Secondaries were thus not included in the description of moult stage M3 in the initial study (paper II). The importance of differences in bleaching and wear was not discovered until photos of wings from the captured birds were analysed (caption 5.6.2). The intensive sunlight to which Snowy Owls are subjected during late spring and early summer before they start moulting, results in gradually stronger fading from the first to the innermost secondaries (Fig 1). If a secondary shows more heavy wear and bleaching further out in the wing than a secondary further in, it is thus usually a feather from an earlier moult category. The images of live captured birds also showed that Snowy Owls moult inner secondaries or tertiaries in the same order as found in Great Grey Owls, with fresh feathers of the second adult generation after third moult M3. Although the new moult interpretations have not yet been published in scientific journals, these new interpretations and descriptions of Snowy Owl moult were presented at the International Snowy Owl Working Group´s third gathering in Boston in March 2017 (Solheim 2017). Nine owls have been recaptured or found dead showing one or several moults. The number of moulted feathers has been demonstrated by comparing patterns of each feather (paper III). These age blueprints include photos of birds in stages M0 - M1 (4 females, 1 male), M0 - M2 (2 females), M1 - M4 (1 female), Mx - Mx+1 (1 female), Mx - Mx+2 (1 female) and Mx - Mx+8 (1 female) (Solheim 2017). The two first categories M0 - M1 and M0 - M2 have confirmed the interpretations of these moult stages as first described in 2011 (paper II).

Both Snowy Owls and Great Grey Owls start their moult with the innermost secondaries and the longest primary. This includes P7 in Snowy Owls and P5 in Great Grey Owls. Snowy Owls moult a varying number of primaries during the first moult, ranging from 0, P7, P7 and P8, or in extensive moults P7-P9 (Fig 7). P6 has never been found moulted during this first moult, but may be included in the second moult. During the third moult some or all of the innermost primaries P1-P4 are usually moulted. In the original moult study (paper II) S2 and S5 were never moulted during M1. This is however often the case in the Snowy Owls photographed in USA and Canada. The state of wear and bleaching of the innermost secondaries help guide whether the owl has moulted once or twice. When the innermost secondaries S8-15 contain adult feathers of two generations, the owl must have moulted twice (Solheim 2017).

The 12 Great Grey Owls in moult stage M1 (paper I) had moulted 1-3 primaries. All except one had moulted P5, six had moulted P4 and nine had moulted P6. One bird had moulted P6-8, with P5 still juvenile. Six of the 12 individuals had moulted S5 during M1, and only one had also moulted S2. One bird had moulted all secondaries from S5 to S11 during the first moult, while the other five with moulted S5 always had at least one juvenile secondary between S5 and the innermost, fresh secondaries.

Both Snowy Owls and Great Grey Owls are subject to differences in sunlight exposure, depending on both habitat and latitudinal differences of an individual's presence. Melanin increases the strength and resistance to wear and bleaching of a feather (Bonser 1995), and dark feathers have more melanin than light feathers. Especially for Great Grey Owls this results in differences in the degree of bleaching between individual owls. While some birds may show clear differences in darkness on wing feathers of different age, such differences may be hard to spot on other individuals, even when they obviously must have feathers of at least two generations in their wings. It is thus of utmost importance to photograph wings of owls under good light conditions to document moult patterns.

The intense sunlight which most Snowy Owls are subject to during spring causes considerable bleaching of dark spots on body plumage feathers. This bleaching can easily create confusions as to how heavily spotted Snowy Owls are as they age, when images of an individual from

Figure 13 Female Snowy Owl satellite tagged on Bylot Island, Canada in 2007, and later photographed in Saskatchewan April 10, 2008 (left image) and January 16, 2010 (right image). Photos: Marten Stoffel.

Figure 14 Female Snowy Owl photographed in Finnmark county, Norway, January 20, 2011. Close inspection of the wing images revealed that there were no juvenile feathers left in the wings, and the owl was thus aged 5CY+. Photo: Ken Göran Ugglebakken.

different times of the year are compared. A female satellite tagged on Bylot Island in Canada in summer 2007 was later photographed in Saskatchewan in 2008 and 2010 (Fig 13). These images made the impression that this bird became more heavily spotted and darker from 2008 to 2010 (Bortolotti & Stoffel 2012). The dark plumage of this female in 2010 was however photographed January 16, while the light plumage in 2008 was photographed April 10 (Marten Stoffel pers. com.). The intense sunlight and snow albedo on the Saskatchewan plains (50^0 45´N) where this bird spent the winters causes heavy bleaching and is most probably the reason why the bird appeared darker in January 2010 than in April 2008. A female Snowy Owl photographed in Finnmark, Norway January 20, 2011 also at first was thought to be a juvenile bird based on the heavy dark spotting on the breast. The wings of the flying bird however showed that it was an adult with no juvenile primaries left (Fig 14, Solheim et al. 2018).

Moult is an energy-demanding process in a bird´s lifecycle (Newton 2009). The production of new feathers depends on the nutritional status of the bird, and is also closely linked to the energetic costs of reproduction (Rohwer et al. 2011, Dietz et al. 2013). Ural Owls moult fewer flight feathers in years when they reproduce compared to years with no reproduction (Brommer et al. 2003). The amount of flight feathers moulted may also influence the reproductive output of owls the following year (Pietiäinen et al. 1984). Owls may thus moult a varying amount of flight feathers depending on the availability of prey and reproductive output. This may explain the difference found in the progress of moult in Eagle Owls between Scandinavia and Spain (Solheim 2011), with more prey available in the owls´ home ranges at southern latitudes. Most of the Snowy Owl skins studied in the museums (paper II) were old and collected during summer at breeding locations. This may explain why none of the 20 individuals in moult stage M1 had moulted any secondaries in the focal points S2 and S5. The wing photos sampled in USA and Canada are birds from winter. Their reproductive status is unknown, and many of these individuals may not have bred the previous summer. This could explain why many of these Snowy Owls moulted more secondaries during M1 than I found in the museum material, with S2 and S5 often included (Fig. 7).

6.2 Feather bar patterns and individuality (paper III)

Once a feather is fully grown it does not change patterns except for fading colouration through bleaching as the feather age (caption 5.3). Even when a wing feather is moulted, the new one may have patterns more similar to the old one than to patterns found in feathers from other bird individuals. Such individuality in feather patterns has been used to identify female Goshawks from moulted feathers of different breeding seasons (Hoy et al. 2016, Selås et al. 2017). In both Goshawk studies the identification was checked against DNA samples of the feathers, and proved to be correct for 94.4 and 96.2% of the individuals, respectively. In my studies on owls I did not try to compare patterns of specific feathers with new post-moult feathers. The identification of individuals was based on comparison of feathers of the same moult year.

Since a single wing feather in Great Grey and Snowy Owls can be retained for up to three or maybe four years before being moulted, images of an owl wing can be compared with other wing images taken within a timespan of up to c$\pm$ 4 years. I have primarily used bar patterns on primaries for such identifications, because more of their vanes are exposed than on secondaries on images of flying birds (paper III). Because Great Grey Owls and Snowy Owls moult wing feathers during summer, all their wing feathers retain their individual bar patterns until the next moult period. This implies that an owl photographed flying in October should show identical wing bar patterns on an image taken in May the following year. Within the same moult cycle all wing images of an owl species can thus be compared for individual bar patterns and identification. Wing images of flying Snowy Owls in Saskatchewan taken within one winter could thus all be compared for individuality (paper III). Images of wings of two juvenile male Great Grey Owls which attended clutches 800 m apart were also identified as different individuals based on bar patterns (paper III).

After a moult the number of retained feathers which have the same bar pattern as before the moult is reduced by the number of moulted feathers. When all wing feathers have been replaced, wing bar patterns may have changed more than the variation found between individuals within one moult cycle. One female Snowy Owl was however identified among six potential candidates after four years, and the identity was confirmed by DNA from moult feathers (Solheim et al. 2018). Two female Great Grey Owls which nested in the same Goshawk nest in 2011 and 2013, respectively, were both hatched in 2010, and could be identified as different individuals based on bar patterns on juvenile feathers P1 and P2 (paper III).

Wing images of captured Great Grey Owls in the age study (paper V) presented 13 opportunities to compare wing images of the same individual two years in a row. The images from the first year were given random numbers so I could match them with the image taken the next year. I compared these images in spring 2019, and all images were matched 100% based on similarities of dark bars and bar patterns on unmoulted feathers.

6.3 Applying moult and feather bar patterns in population studies (paper IV-VI)

I used the methods described in paper I-III to age and identify individual Snowy Owls during a summer invasion (paper IV), nesting Great Grey Owls in an expanding population in SE Norway (paper V), and dispersing Great Grey Owls reported through public sciences approach in a post-breeding year (paper VI).

6.3.1 Snowy Owl summer invasion (paper IV)

Snowy Owls were encountered on the remote Beliy Island north of the Yamal peninsula in Russia. As many as 89 owls were observed from one vantage point during field censuses, and more than 150 owls were probably present in the area censused (paper IV). Owls were photographed along routes crossed on four occasions from 7 to 15 July 2015, and 114 images showed the wings of flying owls. Based on these images a minimum of 25 individuals were aged and sexed, showing that 80% of these owls were young owls hatched in 2012-14.

Digital images are stored with information on time and date when the image is captured. In the Beliy material there was a 4 hour discrepancy between the camera clock and the time registered on the GPS track. When this discrepancy was corrected for, the images selected for aging and sexing could be placed along the survey lines (paper IV). Some of the more advanced system cameras now have GPS built in, so the exact location of an image can be stored as basic image information. Such cameras should thus be used when collecting images to study age and sex distributions of owls in an invasion-like appearance.

Owls must be captured to be banded or checked for former bands. Although captured owls give the best opportunity for taking good wing images, images of flying owls may provide enough information to allow both aging and separation of different individuals (paper III). It would be impossible to trap even a small fraction of the Snowy Owls on the remote Beliy Island for banding and aging purposes. Even if several owls could have been captured, they might not reflect the age structure of the owls during an invasion. Some individuals are always more reluctant to be captured, and trapping thus do not sample a population randomly (Garamszegi et al 2009). Photographs of owls encountered along census lines may better reflect the age and sex distribution of the owls which take part in an invasion. Under the assumption that at least 89, and probably some 150 individual Snowy Owls were present in the census area on Beliy Island in July 2015 (paper IV), the aged birds represent between 16.7% and 28.1% of the surveyed population.

A study on adult Snowy Owls equipped with satellite transmitters in Norway documented that Snowy Owls breeding in Scandinavia in peak lemming and vole years move to Russia as far east as the Taimyr peninsula (75º N 100º E) (Solheim et al. 2008, Jacobsen et al. 2009, 2013), and even to the October Revolution Island (80º N 99º E) (Jacobsen et al. 2014) during years with no or few lemmings in Scandinavia. Twelve Snowy Owls equipped with satellite transmitters in Norway in 2011 moved along the Russian Arctic from Kola Peninsula to Novaja Zemlya and Vaygach Islands in 2012 and 2013, with Novaya Zemlya as the most probable area for breeding (Jacobsen et al. 2013). The young owls which turned up on Beliy Island during summer 2015 were thus most likely the result of Snowy Owl reproduction along the Russian Arctic tundra (paper IV). Because chicks may die late in the breeding season, early surveys of nests with eggs or small chicks can give a false impression on the breeding success of Snowy Owls (Øien et al. 2016). The proportion of young birds which later take part in invasions may thus better reflect the success of breeding efforts in the preceding summer. The method of aging and sexing the owls on Beliy in July 2015 by photographs thus provided new information on breeding success of Snowy Owls along the Russian Arctic tundra in the years 2012-14.

6.3.2 Great Grey Owl breeding population (paper V)

The Great Grey Owl has expanded its distribution in both Scandinavia (Solheim 2009, Berg et al. 2011, 2019) and in North East Europe (Ławicki et al. 2013). Wing photos of captured and free-flying Great Grey Owls were used to study the age distribution of nesting owls as the Great Grey Owl became established as a regular breeding bird in Hedmark County (paper V). A total of 344 nests or breeding attempts were recorded in 2009-2018, and 278 breeding adults were aged based on the moult descriptions (paper I, Suopajärvi & Suopajärvi 1994), of which 53 (19.1%) were aged based on wing images of flying birds. The data set was enlarged by the wing images of non-captured individuals, especially for males which are more reluctant to approach and attack intruders at the nest site and thus less likely to be captured. During the six breeding seasons 2010-11, 2013-14 and 2017-18, 48 Great Grey Owls were handled at least twice (banding and at least one control). These birds gave new information on moult sequences, especially for the stage M3 (caption 6.1, tab. 1) which lacked in the original moult study (paper I).

Since the majority of the birds aged in the Great Grey Owl study were captured, their identity was confirmed by leg-bands. Some individuals were however identified by their wing bar patterns early in the nesting season before any capture attempts, and some non-captured birds were identified as separate individuals based on flight images (paper III; figs 8-11).

The proportion of one year old individuals among the breeding Great Grey Owl was higher in each of the three years preceding the crash in the microtine rodent populations (2011, 2014 and 2018) than in the preceding microtine rodent increase year (2010, 2013 and 2017), significantly so in 2010-2011 and 2017-2018, but not in 2013-2014. The year 2011 was exceptional with 77% of the nesting birds being one year old, compared to only 5% in other years. From 2013 and onwards the proportion of one year old nesters was almost similar to what was found in an established population of Great Grey Owls in northern Sweden (Solheim and Stefansson 2016). In a population of Ural Owls in Finland, 16% of the nesting individuals were 1 year old (Brommer et al. 1998). Here, nesting as a one year old was conditional on being hatched in the pre-peak vole year, 42% of the breeding Ural Owls were one year old in the vole peak year, compared to only 3% in the pre-peak year and 0% in the low year (Brommer et al. 1998). The proportion of one year old Great Grey Owls in Hedmark was much higher in 2011 than in the corresponding peak phase of the two next vole cycles (2014 and 2018). The population density of Great Grey Owls in the study area was far lower in 2011 (22 nestings recorded) than in 2014 (64 nestings recorded) and in 2018 (103 nestings recorded). Thus, the proportion of one year old owls nesting declined as the population density increased. The high proportion of one year old Great Grey Owls breeding in Hedmark in 2011 was probably due to natal dispersal of birds hatched further east in Sweden in 2010. This is also the most likely explanation for the steep rise in nests and nesting attempts in Hedmark from 2010 to 2011 (from 3 to 22). Two females controlled nesting in Hedmark in 2011 and 2017 were both hatched and banded as nestlings in 2010 in Dalarna and Jämtland respectively, and support the hypothesis of natal dispersal from Sweden.

In Swedish studies of Great Grey Owls, nesting birds were aged only if they had been banded as nestlings (Stefansson 1997). This method misses the opportunity to gain precise age data for a larger sample of owls when capturing adult breeders. If moult sequences and the difference between juvenile and adult wing feathers (paper I) had not been applied in the Great Grey Owl studies in Hedmark (paper V), the exceptional high proportion of young breeders in 2011 would not have been discovered. Aging owls by their wing moult patterns thus adds essential information to such population studies.

6.3.3 Great Grey Owls reported through public sciences (paper VI)

The Swedish and Norwegian national species report archives collect data on animals and plants (Artdatabanken.se and Artsdatabanken.no). Both countries use the same digital database, based on the Swedish Species Project started in 2002, where informers can make daily entries of their observations. Many reports are supported by photos of the species observed, which confirm reports to the correct species. This version of public sciences has generated huge amounts of data on a great variety of species, and several millions of entries with locality data are uploaded to and read from the registry every year. The vole peak year 2011 was followed by a crash in the vole populations, with vole depression in most of southern Scandinavia in 2012 (paper V). Many Great Grey Owls were observed hunting in open landscapes and grass fields in 2012, and 4263 single report entries were made to the Swedish species archives (paper VI). I gained access to all reports including restricted reports. Only 107 reports were made from Norway to the Norwegian archives. A total of 813 reports included one or more photos of the observed Great Grey Owl. In 323 of these reports (39.7%) at least one image could be used to age the owl. Based on the locality identities these images were judged to represent 144 different individuals. Most of the owls were photographed perching, allowing for judgement of tail feathers only. Juvenile tail feathers are narrow and pointed with white fringes, while adult feathers are broader and rounded without white fringes. A few reports included images of flying owls, which allowed a more detailed aging based on the moult sequences in their wings. In the age category 2CY+ from autumn 2012, 10 owls could not be judged as whether they were hatched in 2011 or earlier, and were left out in the analyses. At least 102 of 134 individuals (76.1 %) were juvenile owls hatched in 2011. If nine owls judged as likely 2CY birds in spring 2012 were included, the proportion of juveniles were 82.8 %. The high proportion of juvenile owls among the birds observed and reported documents that 2011 must have been a very good reproductive year for Great Grey Owls in southern Scandinavia, as reported from both Sweden (Stefansson 2013) and Norway (Berg et al. 2011). The reports cannot tell whether adult and juvenile Great Grey Owls chose different strategies to cope with diminishing vole populations. Adult birds could be more experienced hunters and stay within old growth forests while the young ones were left to search out new hunting grounds in open landscapes. Adult birds could also migrate in different directions than their progeny. A satellite tagging project was initiated in 2014 with the aim to unveil movement behaviour of adult Great Grey Owls when vole populations crash (Solheim et al. 2015, Solheim 2019b).

6.4 Photography as a non-invasive technique

Taking photos of free flying owls is obviously a less stressful approach than trapping the birds (Zuberogoita et al. 2018). Studies based on the use of photos of free flying birds thus fulfils the considerations of the "3R" (replacement, reduction, refinement) principle (Lindsjö et al. 2016), and reduces the risk of injury or other potentially negative effects. Taking photos of free ranging owls is also cost- and time-efficient compared to trapping the same number of individuals. Since individual animals differ in respect to trappability (Garamszegi et al. 2009), taking photos of individuals for aging and ID recognition may result in more correct sampling of age distributions when studying populations (paper V) or birds during invasions (paper IV and VI).

Photographic techniques and equipment have changed rapidly since photography in the early 2000s went from analogue to digital. Many ornithologists are keen nature photographers and document their observations with images of high quality. The world of digitalization is also changing fast, and it is difficult to anticipate which options the future may present for public sciences. Many photographers and bird observers present their bird photos on Facebook, and such images can often be used both for aging and identification of individuals. During the time since the study of Great Grey Owls was conducted in 2012, mobile phones have become increasingly competitive to compact cameras with respect to image size and quality, and can in many respects even compete in image quality with more expensive system cameras. The world of documentation is thus fast changing, and images captured by smartphones may soon vastly outnumber other photos in the species archives. While images taken with a smartphone are sufficient to document the species of an observed owl, such images rarely allow enough magnification to see details for aging and identity checks. Smartphones are not sufficient to capture good images of flying owls, resulting in too blurry images. The methods I have described and used to age and identify both Great Grey Owls and Snowy Owls are based on sharp images, preferentially of flying birds. Studies from images collected through public sciences may thus be more demanding in the future than they have been hitherto. Similar studies to the ones I have conducted should thus primarily be based on field work by researchers with adequate photographic equipment and training to capture images useful for aging and identification. System cameras with GPS tracking units can provide extra valuable images, as the location of an owl is pinpointed when and where the bird is photographed.

The use of photos to identify owls is limited in time to c± 2-4 years within a full moult cycle. The technique also dependens on field work with adequate photo equipment. Old-fashioned leg banding is still the best method to ensure than an individual can be positively identified and aged after many years, way out of the range of years the image method (paper III) can cover. Telemetry is paramount to disclose movement patterns between breeding seasons of both Snowy Owls (Fuller et al. 2003, Solheim et al. 2008, Jacobsen et al. 2012, 2017, Therrien et al. 2014) and Great Grey Owls (Duncan 1987, Solheim et al. 2015, Solheim 2019b). The use of photos to age and identify owls may thus be a valuable complement to such established methods in the efforts to study and monitor the ecology and population development of these two vole hunters of northern tundra and taiga.

7. Conclusion

I conclude that moult patterns can be used to age Great Grey and Snowy Owls until their third or fourth wing feather moult, as long as at least one juvenile feather is left in the wing. The moult status can be seen on wing images of captured birds, but also on images of free flying birds when the whole wing is visible. Wing images of free flying owls can be used both for aging and identification of individuals. Taking wing images of both captured and free-flying owls adds crucial information for aging birds in population studies. The methods described can also enhance the value of information from images gathered through public sciences.

8. Future perspectives and work

In this study I have shown how moult and wing bar patterns of Great Grey Owls and Snowy Owls can be used to age and identify individual owls, both when captured for banding and when photographed flying free. I have demonstrated that individuals may be recognised even after several moults provided that some wing feathers are retained from time of first to last image. This method has primarily been applied in the Great Grey Owl studies, but should also be useful where Snowy Owls appear on a regular yearly basis. The prairie landscapes of Saskatchewan in Canada provide good opportunities for such studies of free-flying Snowy Owls, as Snowy Owls hunt in these flatlands every winter (Solheim et al. 2014). Photos of Snowy Owls one winter can be compared with photos taken in the same area the next winter, to disclose how many individuals use the same winter area in separate seasons.

In the vole depression year of 2012 in Scandinavia, high numbers of Great Grey Owls hunted in open landscapes outside the breeding area, and were seen and reported by people (paper VI). During the next vole depression year of 2015 Great Grey Owls all over southern Scandinavia seemed to stay within the breeding areas in the coniferous forest, and not hunt in open landscapes (Solheim et al. 2019). After the last two vole years of 2017 and 2018 (paper V), Great Grey Owls have met a new vole depression again in 2019, and many owls have been seen and photographed hunting in open landscapes along the coast of southern Norway. I have searched for, photographed and captured some of these owls, and collected images from the national species archives and Facebook presentations. These images have provided many opportunities for comparing feather patterns to check identity of individuals, and prevent doublecounting of observations. Observations from 2019 will be subject to a study on age structure and the proportion of banded juveniles. Information from captured owls and images disclosing whether an owl is banded or not may be used as a capture-recapture method to calculate the total reproductive output of Great Grey Owls in south-central Scandinavia in 2018.

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PAPER I

The Great Grey Owl that started it all and spurred my curiosity when she displayed her wing, east of Mandal, Agder, October 15, 2009.
Photos: Roar Solheim.

ORNIS SVECICA 21: 11–19, 2011

Moult pattern of primaries and secondaries during first and second flight feather molt in Great Grey Owls *Strix nebulosa*

Mytemønster i vingen hos lappugle Strix nebulosa *etter første og andre svingfjærmyting*

ROAR SOLHEIM

Abstract

Great Grey Owls start flight feather moult when in their second year. Moult was studied on outspread wings of 58 individuals in the collections at Naturhistoriska Riksmuseet in Stockholm. The owls always moulted the innermost secondaries in their first moult, and usually at least two primaries, most often P5 and P6. After this moult, birds had 11–17 juvenile feathers left in each wing, of a total of 21 flight feathers. In their second flight feather moult, birds shed primaries outwards and inwards from the primaries moulted during the first moult. A variable number of secondaries outwards from S10 and S11 were moulted. All birds retained at least one juvenile feather, always P1. The number of juvenile flight feathers after the second moult was 1–6. The collection held no individuals known to be in their third flight feather moult. Thus it was not possible to determine whether birds in this age group could be aged by the wing moult pattern. Great Grey Owls with no juvenile flight feathers should thus be classified as 4C+ in autumn, and 5C+ in spring.

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Introduction

Very little is written on the moult of large feathers in owls. Mikkola (1983) does not cover this field, but in Cramp (1985) moult of flight feathers is described, mostly based on studies of captive birds. Moult is described for Little Owl *Athene noctua*, Tawny Owl *Strix aluco*, Long-eared Owl *Asio otus* and Short-eared Owl *Asio flammeus* in Baker (1983). The fact that Snowy Owls *Bubo scandiacus* and Eagle Owls *Bubo bubo* have 15 or more secondaries, opposed to the other owls which have 10 or 11, is only mentioned by Cramp (1985) as far as I have discovered. Suopajärvi & Suopajärvi (1994) described moult in Great Grey Owls, and Niiranen & Haapala (1987) described moult in Eagle Owl, however both papers in Finnish, and thus not easily accessible.

Large owls and birds of prey do not moult all their flight feathers each year. They usually start moulting some primaries and secondaries in their second summer (second calendar year; 2C). Next year the moult continues, and the birds shed some of the older feathers. In their third moult (as 4C) or even later, the last juvenile feathers are usually lost in the largest species. Smaller species may moult all their flight feathers annually (as in Hawk Owl *Surnia ulula*; Cieslak & Kwiecinski 2009), or partially (as in Tengmalm´s owl *Aegolius funereus*; Cieslak & Kwiecinski 2009, own data).

Through the year, feathers are bleached by sunlight and worn by use. When flight feathers are moulted partially each year, feathers of uneven age will look different in relation to colour, contrast, wear and tear. A pattern of dark and light feathers thus appears. However, the differences between feathers are not always easily observed, unless the bird´s wings are examined in good light conditions (daylight or appropriate artificial light).

In some species juvenile flight feathers are distinctively different from older feathers, while in some others there is hardly any difference at all. When juvenile flight feathers are distinct, a bird may be aged quite accurately as long as such juvenile feathers are still present.

Based on work on Great Grey Owls *Strix nebulosa* in late autumn 2009 (Solheim 2009), I wanted to get a better insight into the moulting pattern of this great owl. This species moults a limited number of primaries and secondaries each year (Cramp 1985), thereby creating very distinct and visible moult patterns in the wings of older birds (see Solheim 2009, 2010). The best place for such studies in Scandinavia is Naturhistoriska Riksmuseet (NRM) in Stockholm. Here bird skins have been made for several decades with one wing loose and outstretched. This makes it possible to study all flight feathers without harming the skin itself. I was kindly allowed to visit the museum 12–15 January 2010, with access to the bird skin collections.

Material and method

I inspected all Great Grey Owls which had been prepared with at least one free wing. Each wing was photographed with the skin's catalogue number to reduce the risk of mix ups during later analyses of the material. Great Grey Owls have 10 primaries like the other owl species, 11 secondaries and three tertiaries. Tertiaries were not included in the analyses. The feathers were numbered starting from the carpal joint, in the same manner as described for Ural Owls *Strix uralensis* by Pietiäinen et al. (1984). The primaries and secondaries of each bird were described as being juvenile, old, new or dark. The last category was used for feathers distinctively different from juvenile feathers, but with too weak differences to be classified as old or new. Juvenile feathers were always easily recognized, because they have distinctly narrow terminal dark bands (see Figure 1). Wings where the contrast between feathers was not obvious, were also watched under UV-light in a dark room. The use of UV light greatly enhances the differences of new and old feathers, at least in some owl species (Solheim in prep.). Although new feathers did not light up under UV light as in owls with lighter feathers, in some cases the UV enhanced differences and underlined similarities between feathers of different and same generations.

Wings from 58 Great Grey Owls were photographed and described (see Appendix 1). For two specimens only the wings had been conserved, and both wings were checked for these two. The owls were recovered all year round, with slightly higher numbers originating from the months April (15), May (7) and October (6) (Table 1). They were classified as belonging to one of four age classes. Birds were classified as juveniles before they started their first flight feather moult in their second calendar year (2C). Juveniles thus include the age categories 1C A (autumn) and 2C S (spring). M1 are birds in or after their first flight feather moult (2C A and 3C S), and M2 are birds in or after their second moult (3C A and 4C S). Birds that have passed through three or more moult cycles, have been classified as 4C+ in autumn, and 5C+ in spring.

A total of 23 owls were ringed, either as pullus (13 ind.), as adults 2K+ (8) or with unknown data for time of ringing (2). Since the birds ringed as pullus can be categorized exactly at time of death, these birds have functioned as a blueprint for the moult pattern study. At time of death, the birds ringed as pullus were in age classes Juvenile (2), M2 (4) and older (7). No ringed birds were thus found in the M1 category. However, as the birds with the highest number of unmoulted juvenile feathers are found here, there is very little risk of

Figure 1. Detail of primaries on specimen 93/6276 from April 1993, showing distinct differences between juvenile and adult flight feathers (P5 and P6). Juvenile feathers are recognized by narrow, often unregular, terminal bands.
Detalj fra håndsvingfjær på lappugle nr 93/6276 fra april 1993. De to lengste mørke fjærene er adulte fra siste sommers myting, og skiller seg tydelig fra de øvrige, juvenile fjærene. De siste kjennes best på smale, ofte irregulære, terminale tverrbånd.

Table 1. Great Grey Owl wings in the collection of NRM, January 2010, showing month of recovery of specimen, and number of individuals in moult categories: Juvenile, M1, M2 and Older. For explanation, see text. Months with individuals in active moult (missing or growing flight feathers), and mean number of moult feathers in respective month is shown. * Individual not included in moult analyzes.
*Lappugler, fordeling på måned funnet, samt alder i kategoriene Juv (1Kh, 2Kv), M1 (2Kh, 3Kv), M2 (3Kh, 4Kv), og eldre (4Kh og eldre). Måned med aktiv myting, og gjennomsnitt antall vingefjær i myting per individ. * utelatt fra myteanalysen.*

	Moult category					Ind. with feathers in growth	Mean no. of flight feathers in moult
Month	Juv	M1	M2	Older	Sum		
January		1		1	2		
February	1		1	2	4		
March	1	1		3	5		
April	2	4	3	6	15		
May		2	3	2	7		
June			1*	2	3		
July			1	2	3	2	6.5
August				1	1	1	2
September	1	2	1	1	5	4	2.5
October	3	1		2	6		
November			1	3	4	1	1
December		1		2	3		
Sum	8	12	11	27	58		

placing these individuals in the wrong category. This conclusion is supported by the described moult pattern (see later). The 7 individuals in the category older birds ranged from 6C to 17C, the last individual being the oldest bird of known age in the material. Since there were no owls of documented 4CA or 5CS age, I have not tried to follow the moulting pattern after the second wing feather moult of the owls.

Time of moult

Eight birds were in active moult, with feathers either missing or growing (Table 1). These birds were recovered in July–September, with an exception of one bird in active moult of P3 found 14 November. Mean number of flight feathers in moult was 6.5 in July, 2 in August and 2.5 in September. Both birds moulting in July were females. However, the number of birds in active moult is too small to indicate any sex difference in moulting period.

First moult M1

Twelve individuals were classified as belonging to this category, with four 2CA birds and eight 3CS birds. The status of their flight feathers is shown in detail in Appendix 2. All individuals moulted at least one primary, but not more than three (mean 2.3–2.4; P6 and P7 of Jno 2008/6726 of uncertain status). Except for one bird, all moulted P5. Nine moulted P6, and 6 moulted P4. P1–P3, P9 and P10 were not moulted in any of these individuals. All birds moulted the innermost secondaries S10 and S11. In 75% S9 was moulted, and 50% of the birds also moulted S8 and S5. No birds moulted S1 and S3, and only a few moulted the rest of the secondaries. The birds moulted 4–10 flight feathers per wing (mean number 6.8–6.9; see above). This means that a Great Grey Owl after its first flight feather moult (2CA and 3CS) has a mean of 14.3 juvenile flight feathers left in each wing (span 11–17).The moult pattern of a bird in this stage is thus easily recognized (see Figure 2).

Second moult M2

Eleven individuals were classified to this category, however one of these (Jno 97/6355) were left out from the analyses due to difficulties of correct numbering of the feathers. Two individuals were 3CA birds, and eight were 4CS birds. Four of the individuals were ringed as pullus, thus confirming their age. The detailed status of the moult patterns of the 10 birds are shown in Appendix 3.

Six of the birds had moulted primaries both out-

Figure 2. Typical wing pattern of a Great Grey Owl (specimen 85/7270) in stage M1, age 2C autumn. This bird has moulted the three primaries P4–P6, the innermost secondaries S9–S11, and S5.
Karakteristisk mytemønster hos lappugle i stadium M1 (alder 2Khøst). Fuglen har mytt håndsvingfjærene P4-P6, og armsvingfjærene S9-S11, samt S5.

Figure 3. Typical wing pattern of a Great Grey Owl (specimen 94/6127) in stage M2, from April (age 4C spring). P2–P4, P7 and P8 were moulted last summer, P5 and P6 were moulted one year earlier, while P1, P9 and P10 are still juvenile, unmoulted feathers. For further explanation on the secondaries' pattern, see Appendix 3.
Karakteristisk mytemønster hos lappugle i stadium M2 (alder 4Kvår). For nærmere forklaring på mytemønsteret, se Appendix 3.

wards and inwards from the primaries moulted the previous year. Most probably all individuals moulted like this, however for four birds the outermost primaries were only categorized as Dark, positively not juvenile feathers. All ten birds had moulted P5 during their previous, first flight-feather moult, and all birds moulted P3 during the second moult. Eight birds also moulted P4 in the second moult, while the two other birds had moulted this primary during their first moult. All birds retained at least one juvenile feather, and for all birds P1 was juvenile. The number of juvenile feathers ranged from 1–6 (mean number 3.4). Considering the 6 individuals in Appendix 3 with the least number of feathers in category D, the owls moulted 6–9 (7–13 if D-category feathers are considered new) flight feathers in their second moult (mean 7.3–10.3).

Because of added effect from individual variation in the number of feathers moulted during M1 and M2, the moult patterns of wings after the second moult (3CA) display considerable variation. In some birds the feathers from M1 and M2 were clearly different in darkness and wear, but in other individuals a considerable number of these feathers could only be classified as Dark (meaning positively non-juvenile). A typical wing of a bird in this category is shown in Figure 3.

Discussion

The moult patterns of Great Grey Owls as revealed by the skin material at NRM, are in accordance with the description given in Cramp (1985), with moult of primaries starting with P5 or P6. The number of Juvenile feathers in the wing after first and second moult does not overlap, and makes it quite easy to recognize these two age classes (Figure 4 and 5). Because there was no skin material available of Great Grey Owls of documented age in or after their third moult (4CA + 5CS), it is not possible for me to find the definitively end of presence of juvenile feathers. However, two ringed 6CS birds had no juvenile feathers left, and neither did any older birds. Juvenile feathers are thus always present at least until birds are in stage 4CS, and seems never to be present after the fourth moult (M4). Until birds in stage 4CA+5CS are studied in detail, Great Grey Owls with no juvenile feathers in their wings should be aged as 4C+ in autumn, and 5C+ in spring (January–June). This is in accordance with Suopajärvi & Suopajärvi (1994), who state that the last juvenile flight feathers are moulted in the fourth or fifth calendar year of Great Grey Owls. According to these authours, the last juvenile flight feathers to be moulted are P 1 or P 10, and S 1 or S 4.

Great Grey Owls moult fewer flight feathers during their first moult than Ural Owls (see Pietiäinen et al. 1984). This may be because renewal of flight feathers is more energy demanding for large owls than for smaller owls. The moult cycle of the larger Eagle Owl seem to be even slower than in Great Grey Owls (Niiranen & Haapala 1987, own studies). In Ural Owls the number of flight feathers

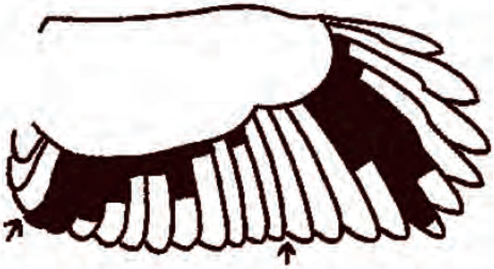

Figure 4. Schematised moulting pattern for the first flight feather moult in Great Grey Owl, based on 12 museum specimens. Black: new feathers, white: juvenile feathers. Proportion of black denotes probability for feather in that position to be moulted.

Skjematisert mytemønster for lappugle etter første svingfjærmyting, basert på 12 museumseksemplarer. Sort: nye fjær, hvitt: juvenile fjær. Mengden sort angir sannsynligheten for at en fjær i denne posisjonen har blitt skiftet.

Figure 5. Schematised moulting pattern for the second flight feather moult in Great Grey Owl, based on 10 museum specimens. Black and white as in Figure 4, hatched: moulted during first moult, spotted: feather either new or from last moult, but positively not juvenile.

Skjematisert mytemønster for lappugle etter andre svingfjærmyting, basert på 10 museumseksemplarer. Sort og hvitt som på Figur 4, tverrstreket: byttet under første svingfjærmyting, prikket: fjær fra første eller andre svingfjærmyting, men tydelig ikke-juvenil.

moulted increase from M1 to M2, then drops from the second to the fifth moult, possibly because increased energy demands when birds enter breeding status (Pietiäinen op. cit.). Although the number of moulted feathers in M1 and M2 are lower in Great Grey Owls, this species too moult more flight feathers during M2 than during M1.These birds have probably not entered breeding status, and the more intense moult in 3C birds may reflect a general phenomenon, or maybe the fact that older birds are better hunters and thus in better condition than one year earlier.

The very distinctive moult patterns in Great Grey Owl wings in age categories 2CA–4CS are usually very easily detected on live birds from a distance, when they stretch their wings or fly. Modern digital photography makes it easy to capture and instantaneously analyze such images. The differences of owls make it possible to identify individual Great Grey owls during field observation (see Solheim 2009, 2010). This owl species is a very good candidate for such field identifications, because Great Grey Owls display a high degree of acceptance to human observers. Being active during daylight, Great Grey Owls are often spotted by people in general, and by ornithologists in particular. As many ornithologists are also active bird photographers, it is possible to actively try to shoot images of their wings during flight, and thus build an identification archive as have been done for whales (see Hamilton et al. 2007) and large conspicuous terrestrial mammals.

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I thank Naturhistoriska Riksmuseet in Stockholm for permission to study their collections of owl wings, and Göran Frisk in particular for finding material and providing data sheets of the skins. Also thanks to Tord Fransson for providing recovery data for ringed owls, and to Pertti Saurola who sent me information on Finnish papers on owl moult. The Norwegian Directorate for nature management provided funds to cover travel costs, of which I am very grateful.

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Opsummering

Som hos andre store ugler myter lappuglene vingefjær partielt, dvs. de skifter bare noen av vingefjærene hvert år. De første vingefjærene mytes når fuglen er ett år gammel, dvs. 2K (i sitt andre kalenderår). Lappuglas første sett av vingefjær er tydelig forskjellige fra de fjærene som kommer etter, noe som gjør det mulig å gjenkjenne juvenile vingefjær. Naturhistorisk Riksmuseum i Stockholm har de beste samlingene i Norden for å studere fuglers mytemønster, fordi fugl gjennom mange år har blitt skinnlagt med en frilagt, utspent vinge. I januar 2010 besøkte jeg museet, og fotograferte og analyserte vinger fra 58 lappugler (Tabell 1, Appendix 1). Av disse var 23 individer ringmerket, derav 13 som reirunger. Mytemønsteret hos disse fuglene har fungert som fasit ved analysen av de øvrige lappuglenes mytemønster (karakteristiske mytemønster i Figurer 1–3).

Materialet omfattet 12 fugler etter første svingfjærmyting (2K.høst og 3K.vår; Appendix 2) og 10 fugler etter andre svingfjærmyting (3K.høst og 4K.vår; Appendix 3). Samlingen hadde ingen fugler med kjent alder etter tredje svingfjærmyting (4K.høst, 5K.vår), og mytemønster er derfor ikke forsøkt kartlagt etter andre svingfjærmyting. Etter første svingfjærmyting hadde alle lappuglene skiftet de innerste armsvingfjærene S11 og S10. De fleste fuglene hadde også skiftet minst to håndsvingfjær, vanligvis P5 og P6. Etter første svingfjærmyting hadde fuglene i snitt 14.3 juvenile vingefjær tilbake i hver vinge (variasjon 11–17), av et totalt antall på 21 vingefjær. I sin andre svingfjærmyting skifter fuglene håndsvingfjær utover og innover fra de fjærene som ble skiftet året før. Et varierende antall armsvingfjær skiftes utover i vingen fra S10. Alle lappuglene hadde minst en juvenil svingfjær tilbake etter den andre svingfjærmytingen, og hos alle fuglene var P1 fremdeles juvenil. Antall juvenile svingfjær i vingen etter andre svingfjærmyting var i snitt 3.4 (variasjon 1–6). Mangelen på ringmerkte fugler med kjent alder i kategorien 4K.høst/5K.vår umuliggjorde vurdering av om mytemønsteret kan følges hos lappugle etter den tredje svingfjærmytingen. Lappugler som helt mangler juvenile svingfjær (med hovedvekt på P1), bør derfor aldersklassifiseres som 4K+ på høsten, og 5K+ på våren.

Det tydelige mytemønsteret hos lappugler i alderskategoriene 2K.høst–4K.vår kan lett gjenkjennes på flygende fugler, eller på fugler som strekker den ene vingen (skjematiserte mytemønster i Figurer 4–5). Moderne digitalfotografering muliggjør en umiddelbar analyse av uglenes vinger. Forskjeller i mytemønster og fjærenes flekkmønster gjør det mulig å gjenkjenne lappugleindivider ute i naturen. Lappugla er en spesielt god kandidat for slik feltidentifisering, fordi fuglene vanligvis aksepterer mennesker som ikke kommer for nær. Som dagaktiv jeger observeres lappuglene raskt av mennesker generelt, og spesielt av ornitologer. Siden mange av dagens ornitologer også er gode fuglefotografer, kan en aktivt oppfordre alle til å forsøke å samle fotografier av lappuglenes vinger, og på den måten bygge opp et identifikasjonsarkiv slik man lenge har gjort for bestander av hvaler og store, lett observerbare, landlevende pattedyr.

Appendix 1.
Great Grey Owls in the collection of NRM photographed in this study. Museum journal number, date of recovery, classification in moult class and age at time of ringing for ringed individuals. Ages in bold: confirmed age of birds ringed as pullus. K=calendar year, S=Spring, A=Autumn.
Lappugler fra NRM fotografert i dette mytestudiet. Museets journalnummer, dato for funn, alderskategori og alder ved merking for ringmerkte individer. Uthevet skrift: kjent alder.

J.no NRM	Date	juv	M1	M2	Older	Ringed as
76/0191	14.5			4KS		
78/6043	11.5		3KS			
82/6418	10.9			**3KA**		pull.
84/6137	12.2	2KS				
84/6186	25.3	2KS				
84/6187	19.3				5K+?	2K+
84/6370	13.5		3KS			2K+
85/6359	31.3		3KS			
85/6399	5.4	**2KS**				pull.
85/6957	14.7				5K+	
85/7253	16.9	1KA				
85/7270	22.9		2KA			
85/7454	16.10		2KA			
85/7482	22.10				5K+	
85/7600	26.6				**6K**	pull.
86/6246	7.4				**6K**	pull.
86/6284	15.4		3KS			
86/6319	24.4	2KS				
86/6321	2.5			4KS		
86/6379	28.4		3KS			
87/6203	12.4			**4KS**		pull.
87/6235	22.4				5K+	
87/6274	9.4			4KS		
87/6738	14.11				**7K**	pull.
88/6144	30.4				**8K**	pull.
88/6376	8.5				5K+	2K+
89/6052	16.2				5K+	
90/6536	26.11				5K+	
91/6159	7.5			4KS		
91/6433	14.6				**8K**	pull.
92/6125	15.4				4K+	2K+
92/6224	7.10	1KA				
93/6276	13.4		3KS			
93/6911	28.10				5K+	
93/6966	16.11				5K+	
94/6127	4.4			**4KS**		pull.
95/6048	9.2			4KS		
95/6104	Apr				5K+	
95/6140	19.12				5K+	
95/6141	26.3				5K+	
95/6312	2.7				**5K+**	2K+
95/6465	Nov			3KA		
95/6533	Dec		2KA			
96/6332	20.5				**12K**	pull.
97/6080	3.3				**17K**	pull.
97/6107	2.4		3KS			
97/6355	19.7			3KA		?
2000/6024	10.1		3KS			
2000/6086	3.9				5K+	
2001/6256	18.6			**4KS**		pull.
2002/6458	9.10	1KA				
2003/6153	10.2				5K+	
2004/6425	13.4				**12K+**	3K+
2005/6512	29.10	**1KA**				pull.
2005/6516	31.8				5K+	2K+
2008/6726	17.9		2KA			
2009/6006	3.1				**8K+**	2K+
2009/6013	22.12				5K+	?

Appendix 2.

Moult pattern of 12 Great Grey Owls in stage M1 (2Ca or 3Cs). JNo refer to the Museum catalogue number at NRM. N: New, fresh feather, N(-): New, but more bleached than other feathers in same category, Small letter: growing feather, J: Juvenile feather. *: Both wings analyzed. Juv: number of juvenile feathers in wing of individual. Bottom lines: Number of juvenile and fresh feathers after first flight feather moult.

*Mytemøster hos 12 lappugler etter første svingfjærmyting (stadie M1), alder 2Kh eller 3Kv. Jno: Museets journalnummer, N: Ny, fersk fjær, N (-): Ny fjær, men bleket mer enn øvrige i samme kategori, liten bokstav: fjær i utvekst, J: juvenil fjær. *: begge vinger analysert. Juv: antall juvenile svingfjær. Bunnlinje: antall juvenile og nye fjær etter første svingfjærmyting.*

JNo	Primary number *Håndsvingfjær nr*										Secondary number *Armsvingfjær nr*											juv
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	
78/6043	J	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	N	N	17
84/6370	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	17
85/6359	J	J	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	16
85/7270	J	J	J	J	N	N	N	J	J	J	J	J	J	J	N	J	J	J	N	N	N	14
85/7454*	J	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J/N	N	N	16
86/6284	J	J	N	N	N	J	J	J	J	J	J	J	J	N	N	J	N	N	N	N	N	11
86/6379	J	J	J	J	N	N	N	J	J	J	J	J	J	J	N	N	N	N	N	N	N	11
93/6276	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	16
95/6533	J	J	J	J	N	N	N	J	J	J	J	J	J	J	N	J	J	N	N	N	N	13
97/6107	J	J	J	J	N	N	N	J	J	J	J	J	J	J	J	N	J	N	N	N	N	13
2000/6024	J	J	J	J	N	N	J	J	J	J	J	J	J	J	N	J	J	N	N	N	N	14
2008/6726	J	J	J	n	n	N	J	J	J	J	J	N	J	J	N	J	J	J	N	N(-)	N(-)	13
Juv	12	12	12	10	3	1	6	12	12	12	12	11	12	11	6	10	10	6	2,5			
New			1	2	9	11	6							1	6	2	2	6	9,5	12	12	

Appendix 3.

Moult pattern of 10 Great Grey Owls in stage M2 (3Ca or 4Cs). JNo refer to the Museum catalogue number at NRM. O: Old feather, not from last moult, N: New, fresh feather, D: Dark feather (old or new, but not juvenile), J: Juvenile feather, small letter: growing feather. Juv: number of juvenile feathers in wing of individual. Bottom lines: Number of juvenile feathers, or feathers from first (1M) or second (2M) moult. 1M/2M: feather either from 1M or 2M (category D). *Mytemønster hos 10 lappugler etter andre svingfjærmyting (stadie M2), alder 3Kh eller 4Kv. Jno: Museets journalnummer. O: gammel fjær, tidligere enn siste myting, N: Ny, fersk fjær, D: mørk fjær (gammel eller ny, men ikke juvenil), J: juvenil fjær, liten bokstav: fjær i utvekst. Juv: antall juvenile svingfjær. Bunnlinje: antall juvenile svingfjær, og vingefjær fra første (1M) eller andre (2M) svingfjærmyting. 1M/2M: fjær fra enten første eller andre svingfjærmyting (kategori D).*

JNo	Primary number *Håndsvingfjær nr*										Secondary number *Armsvingfjær nr*											juv
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	
76/0191	J	J	J	N	O	O	N	N	J	J	J	D	D	D	D	D	D	D	D	D	D	6
82/6418	O	n	n	O	O	O	N	N	N	J	D	D	D	J	D	D	D	D	D	D	D	2
86/6321	D	D	D	D	O	O	N	N	J	J	N	O	N	N	O	N	N	O	O	O	O	2
87/6203	D	D	D	D	D	O	N	N	J	J	J	O	D	D	D	D	D	D	D	D	D	3
87/6274	J	J	D	D	D	O	N	N	J	J	N	N	N	N	D	O	N	N	O	O	O	4
91/6159	D	D	D	D	O	O	O	N	J	J	N	N	N	N	O	O	O	N	O	O	O	2
94/6127	J	J	N	N	O	O	N	N	N	J	J	N	N	J	O	O	O	O	O	O	O	5
95/6048	J	J	N	N	N	O	N	N	J	J	J	N	N	J	D	D	D	D	D	D	D	6
95/6465	J	J	N	N	N	O	O	N	N	J	N	O	N	N	O	O	N	O	O	O	O	3
2001/6256	N	N	N	N	O	O	N	N	N	J	D	D	D	D	D	D	D	D	D	D	D	1
Juv	5	5	1						6	10	4			3								
1M	1			1	6	10	2	10				3			4	4	2	3	5	5	6	
2M	1	2	5	5	2		8		4		4	4	6	4		1	3	2				
1M/2M	3	3	4	4	2						2	3	4	3	6	5	5	5	5	5	4	

PAPER II

Dan Zazelenchuk releasing a juvenile, 2CY male Snowy Owl in Saskatchewan, Canada, February 16, 2016. Photo: Roar Solheim.

Wing feather moult and age determination of Snowy Owls *Bubo scandiacus*

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Abstract. Moult of primary and secondary flight feathers of Snowy Owls *Bubo scandiacus* was studied from 53 museum specimens retaining some juvenile feathers. There were no ringed Snowy Owls of known age in the skin material, and the moult pattern has thus been interpreted using the moult of Eagle Owls *Bubo bubo* as a model. The difference between juvenile and adult primaries is described. Greater coverts may facilitate age determination of single flight feathers. Snowy Owls start their first flight feather moult M1 by shedding the innermost 2-6 secondaries during their second summer (as 2C birds). A majority of the owls also shed primary P7 during this first moult, occasionally also P8. This moult progresses at a faster pace than seen in Scandinavian Eagle Owls. During their second flight feather moult M2, moult of secondaries advances outwards, including moult from the two focal points S2 and S5, as in the Eagle Owl. Both P7 and P8 are moulted and fresh after M2, and some owls even moult P6 or P9. After the third flight feather moult M3 it is very hard to distinguish juvenile secondaries from old M1 secondaries, and a specific moult pattern is most easily recognized in primaries. On sharp images of the upper side of wings on a flying Snowy Owl, or on birds in hand, it should be possible to age birds up to four calendar years (4C) in autumn and five calendar years (5C) in spring, before onset of the fourth flight feather moult M4.

Key words: owls; snowy owl; moult; ageing

INTRODUCTION

With the exception of Tamaulipas Pygmy Owl *Glaucidium sanchezi*, the Snowy Owl *Bubo scandiacus* is the only owl species with distinctive sexual dimorphism in plumage (del Hoyo et al. 1999), with males being more white and unspotted than females. There are several descriptions of the plumages of Snowy Owls, and how to sex and age them (Portenko 1972, Josephson 1980, Cramp 1985, Olsen & Fredriksson 1992). However, there are substantial individual variations in plumage within the same sex and age groups, with a great potential for making misjudgements. In 2003-2004 I photographed all (approximately 400) Snowy Owl skins in the main Natural History Museums in Norway, Sweden, Finland and Denmark to review the sex and age categorization of this material (Solheim et al. 2004). I soon realized that the individual variation of these birds is quite complex, and that ageing and even sexing of Snowy Owls is not as straight forward as described. The reviewing of the skin material has thus undergone several revisions, especially after discussions with other people with extensive field experience from working with Snowy Owls.

MATERIAL AND METHODS

The study is based on skins from the Natural History Museum of Stockholm (NRM), the Zoological Museum of Oslo (ZMO), the Zoological Museum of Copenhagen (KZM) and the Smithsonian Institution, Washington (SMS). A specimen from the Zoological Museum, Helsinki (HZM) is also incli\uded. I examined a total of 378 Snowy Owl skins, of which 53 birds had recognizable juvenile feathers making a categorisation possible. There were 20 males and 33 females. The material covered the whole Arctic, with skins from Greenland (20), Norway, Sweden and Denmark (14), Iceland (1), North America (9) and Russia (5). Four skins lacked data on locality. No major differences seem to exist in the flight feather moulting pattern between males and females. A study of moult in Eagle Owl was done on skin material from the Natural History Museum of Stockholm (NRM), which holds a substantial number of Eagle Owl skins from ringed birds with confirmed age (Solheim 2011b). There were no ringed Snowy Owls in any of the museum collections I visited. I used the sequence of wing feather moult during the first moults of Eagle Owls as a reference for grouping the Snowy Owls into moult groups of similar patterns.

Most recent skins at NRM have been prepared with one free, outspread wing, perfect for wing feather moult studies. However, as most Snowy Owl skins are quite old (100+ years), the vast majority of these skins are made with both wings folded along the body of the bird. To study differences in moult patterns of such wings you have to carefully spread out some of the flight feathers one by one to compare differences in dark spots and hue, wear and bleaching. This can be done with the primaries without harming the skin, and it is also possible to photograph these feathers. The secondaries are however harder to study, because you must carefully bend out one or a few feathers at a time, taking care not to damage the skin. It is not possible to get good photos of the secondaries of such skins. A few recent Snowy Owl skins have however been made with one outstretched wing, and these provide some good examples of the first moult of secondaries.

I have used the ageing categories for birds proposed by Runde (1991). A bird is said to be in its first calendar year (1C) from the time of hatching until 31 December. In the following year it is 2C, and so on. A bird of unknown age, but at least in its X calendar year, is termed XC+. I have added the suffixes "a" (autumn) for birds found in July-December, and "s" (spring) for birds found in January-June. During summer of their second year of life (2C), Snowy Owls moult their first flight feathers, and this moult is termed M1. Next year they enter M2, and so forth.

In the Great Grey Owl *Strix nebulosa* and Eagle Owl, there is a distinct difference between juvenile and later wing feathers (Solheim 2011a, b). As long as some juvenile feathers can be found in the wing, it is possible to age the bird. When all wing feathers have been moulted once, it is not possible to judge the correct age of the bird after 4C/5C for Great Grey Owls, and 5C/6C for Eagle Owls. In Snowy Owls I was able to distinguish between juvenile and adult primaries, especially when both types are present in a wing. Also primary and secondary coverts usually show distinctive juvenile and adult patterns. For the secondaries I was not able to recognize a distinctively juvenile pattern. However, as feathers age, it is usually possible to see if there are two, and sometimes three, age classes of secondaries in the wing. The pattern of dark spots or bands may also act as a clue to distinguishing feathers of the same age class. Coverts are usually moulted together with the underlying primary or secondary. As greater coverts seem to show a more distinctive difference between juvenile and adult feathers, they can act as a clue to judging the status of the secondaries. Also the ageing of problematic primaries can be eased by the status of the primary coverts.

Four birds from July were not included when making the moult schemes, because these birds may not yet have completed their wing feather moult, and as such may show a pattern that could be misinterpreted.

Recognizing juvenile feathers

Juvenile primaries often show mottling between the dark bands towards the tip of a feather. Such mottling is common in both males (Appendix 1.1) and females (Appendix 1.2). There is however considerable variation, and some birds may show very little or no mottling at all, resembling much older birds. Mottling in the coverts may help to reveal the true feather status in such individuals (Appendix 1.3). The primaries and secondaries of juveniles also show an even pattern of spots and bands, with no abrupt changes from one feather to its neighbours. Juvenile primaries are more pointed than primaries of later generations, but these differences are most easily detected when both generations are still present in the wing. However, with experience, it should be possible to recognise a single, juvenile primary feather. In both males and females the terminal dark band of the primaries P7-10 extends almost to the tip, with a very narrow white fringe which may be missing in a few individuals (Appendix 1.1 and 1.2). In females the dark bands stretch across both outer and inner vane, while in males the band usually stops halfway across the inner vane. In older feathers the inner vane bands are usually shortened (females) or completely lost (males).

The secondaries of juveniles are evenly spotted and show no abrupt differences between feathers (Appendix 1.3 and 1.4). In spring from March the tertials and innermost secondaries become gradually more worn and bleached, until they are almost worn down to white in June (Appendix 1.3 and 1.4). This bleaching and wear seems to be more heavily expressed in juveniles than in many older birds.

In the moult pattern scheme non-moulted secondaries have been termed as juveniles in the 2Ca/3Cs birds. In later stages, feathers are termed O (old) in contrast to N (New). In moult category M2 (3Ca/4Cs), any "old" secondary S11-S16 has been judged to be a formerly moulted, non-juvenile feather, while the rest of the "old" secondaries are judged to be juvenile. This interpretation is based on the moult pattern of secondaries in Eagle Owls after M2 (Solheim 2011b).

Recognizing non-juvenile feathers

The first non-juvenile primaries and coverts are usually recognized by the lack of mottling between dark bands. This is best seen when new feathers contrast neighbour, juvenile ones, both in coverts (Appendix 1.5) and in primaries (Appendix 1.6). The tip of a non-juvenile primary appears more rounded as opposed to juvenile

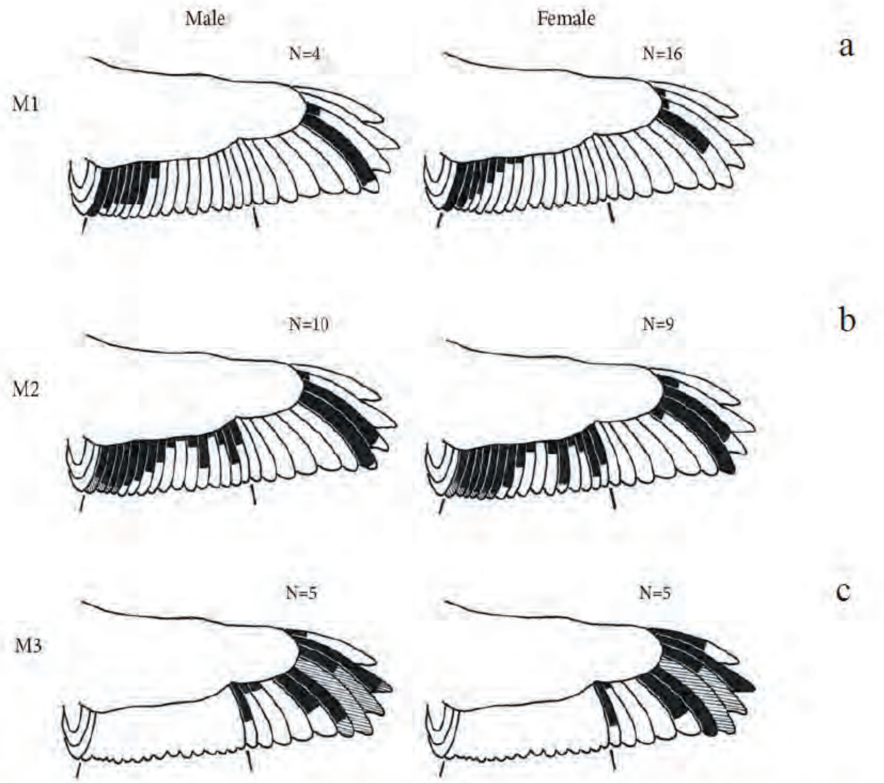

Figure 1. Schematised pattern of first (M1) and second (M2) flight feather moult, and third (M3) moult of primaries of male and female Snowy Owls, based on studies of skinned museum specimens. The amount of black on each feather indicates the proportion of individuals having moulted this feather at this stage. The amount of white indicates the proportion of individuals with juvenile feathers. Hatched indicates proportion of non-juvenile feathers moulted during the previous moult phase. Tertials, and secondaries of M3 are not included in the analysis (see also Appendix 1 for details).

primaries, a feature that is underlined by a broader terminal white fringe (Appendix 1.5 and 1.6). Usually the white fringe of a non-juvenile feather is markedly broader than in juvenile feathers, which may lack a white fringe altogether (Appendix 1.7). However, sometimes non-juvenile primaries may only be distinguished from juvenile ones by their lack of wear and bleaching as opposed to neighbouring feathers (Appendix 1.8). In females the distance between dark bands on the primaries may increase as opposed to the first, juvenile primaries, and the band usually extends only halfway across the inner vane of the feather (Appendix 1.9). Also in males the number and length of terminal dark bands may decrease from juvenile to next generation primaries, but the distinction may be harder to recognize than in females (Appendix 1.10). New primaries also in males usually get a broader, white fringe than on juvenile feathers (Appendix 1.11).

RESULTS

First moult M1

The Snowy Owls start their flight feather moult with the tertials and innermost 2-6 secondaries (Figure 1a, Appendix 2). The four males judged to be in this category had all lost primary P7 on both (3) or at least one (1) wing. The last bird was however from 16 August, and may not yet have completed moulting. One male had also moulted P8, on his right wing only. There were 19 females with the same pattern of secondaries moult, and thus judged to be in the first moult category. Of these, 10 had not moulted any primaries, while 9 had moulted primary P7. One female had also moulted P8 and P9, however on one wing only. At this stage it is very easy to see the difference between P7 and P6, because the tip of P6 is very exposed on a resting bird, and heavily bleached and abraded. This feather will also stick out as more worn than P7 in 2Cs birds before their first wing feather moult. Moult pattern in both wings was checked on 20 of the 23 M1 birds. Of these only 6 showed asymmetrical moult patterns.

Second moult M2

In their second wing feather moult (as 3C birds), all birds had moulted P7, and most had moulted P8 (Figure 1b, Appendix 2). One male and two females had also moulted P9. The birds had now started moulting secondaries from the same two focal points (S2 and S5) as seen in Eagle Owls. From the innermost part of the wing, moult advanced outwards. In males S13-S16 were now completely moulted, while in females S11-S16 were all moulted. Nine of 19 birds had moulted S1, and only one bird had moulted S7. All birds had now moulted P7 (one bird had moulted P7 on one wing only), and most birds had also moulted P8. Some had even moulted P6 or P9. One female had moulted both P6 and P9. Moult pattern could be checked for both wings on 18 of the 19 M2 birds, and 11 of them showed asymmetrical patterns.

Third moult M3

At this stage I have only drawn moult patterns of the primaries (Figure 1c), because it is almost impossible to judge if an old, abraded secondary is a non-moulted juvenile feather, or a moulted feather from M1 or even M2 (but see Appendix 2). After M3 all birds had moulted P6-P9, with P7 (and P8 in some birds) standing out as clearly lighter and more worn than the neighbouring, fresh primaries of N2 generation (Appendix 1.12). More than half of the birds had started moulting from P1, and had also lost P5. The feature separating this moult category from the previous M2 is the marked contrast in hue and abrasion between P7-8 and the newly moulted primaries both inwards and outwards, and the start of moulting from P1 outwards. In all birds P4 was still juvenile, and for most birds also P2 and P3. Moult was checked on both wings for 10 of the 11 M3 birds, and all showed asymmetrical moult patterns.

DISCUSSION

Based on the moult schemes presented here, it should be possible to determine the age of Snowy Owls up to 4Ca/5Cs with certainty. It may even be possible to follow the moult pattern into stage M4, provided that some juvenile feathers are still present in the wing. Extensive collecting of wing photos of live birds could probably help to determine if ageing is possible at this stage. To correctly age a bird with a fresh non-juvenile P7 one should get good views of the outer half of the secondaries. A bird with homogenously patterned secondaries S1-S8 should be aged 2Ca/3Cs, while a bird with fresh, non-juvenile secondaries S2 and S5 should be aged 3Ca/4Cs.

The material in this study included birds from all major parts of the species´ Holarctic distribution. The Snowy Owl is a monotypic species with no distinctive subspecies or subpopulations, a conclusion also supported by DNA studies (Marthinsen et al. 2008). One should thus not expect to find marked differences in moult patterns in birds from different parts of the Holarctic, as pointed out also by Pyle (1997).

The sequence of flight feather moult found in this study follows the same pattern as that described by Pyle (1997), however Pyle did not recognize the distinctive two focal points of secondaries S2 and S5 for Snowy Owls or other *Bubo* species. These focal points are very distinctive during second moult M2 for both Snowy and Eagle Owls (Solheim 2011b). The proportion of birds with asymmetrical moult pattern when comparing right and left wing steadily increased from M1 to M3, with all M3 birds being asymmetrical. Also Pyle (1997) found that most of the Snowy Owls and Great Horned Owls *Bubo virginianus* studied in North America showed asymmetrical moult patterns after M3.

In the Swedish Eagle Owl material, the birds only moulted the innermost secondaries S13-S15 during their first flight feather moult (Solheim 2011b). Spanish Eagle Owls however also moulted one or two primaries (P7 and P6) during their first wing feather moult (Blasco-Zumeta 2010). Difference in prey abundance between Scandinavia and Spain may explain why Spanish Eagle Owls moult at a quicker pace than the more northern birds. Snowy Owls with no moulted secondaries in focal points S2 and/or S5 are thus more likely to be in moult stage M1 than M2, although they may have started moulting primaries P7 (and in some events even more primaries). Snowy Owls thus seem to have a more extended M1 moult than northern Eagle Owls. Also the moult pattern after M2 supports this interpretation of the Snowy Owl moult. Both during breeding and in their winter habitats, Snowy Owls inhabit more extreme ecosystems than northern Eagle Owls. It is thus puzzling that their first wing feather moult seems to include more feathers than in Scandinavian Eagle Owls.

In Ural Owls *Strix uralensis* the number of moulted flight feathers has been shown to be negatively correlated with the number of offspring produced by the adult during the same summer (Pietiäinen et al. 1984). Since neither Snowy Owls nor Eagle Owls are likely to start breeding during their second year, it is unlikely that the variation in number of moulted flight feathers in stage M1 (and even M2) is linked to reproductive investment. Although Snowy Owls inhabit more extreme breeding habitats with fewer potential prey species than Eagle Owls, they are not bound to a fixed territory like Eagle Owls. The nomadic behaviour of Snowy Owls may thus allow them better nutritional resources than the larger stationary Eagle Owl.

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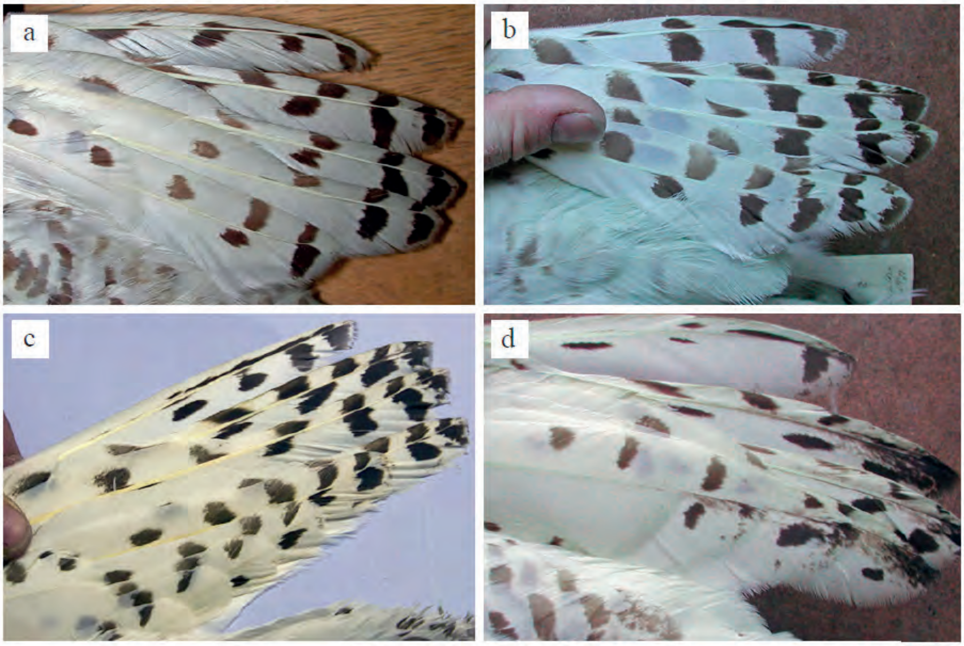
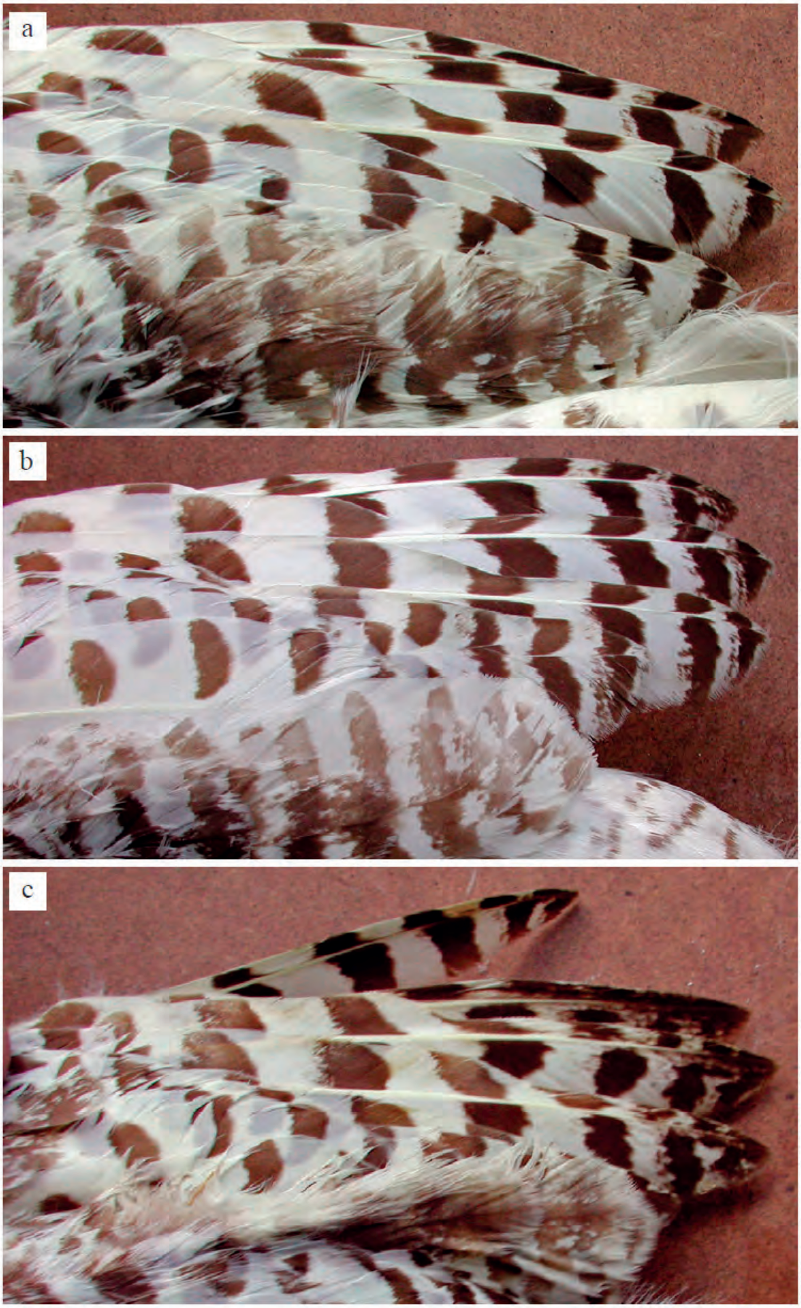
Appendix 1. Moult patterns in Snowy Owl wings according to sex and age.

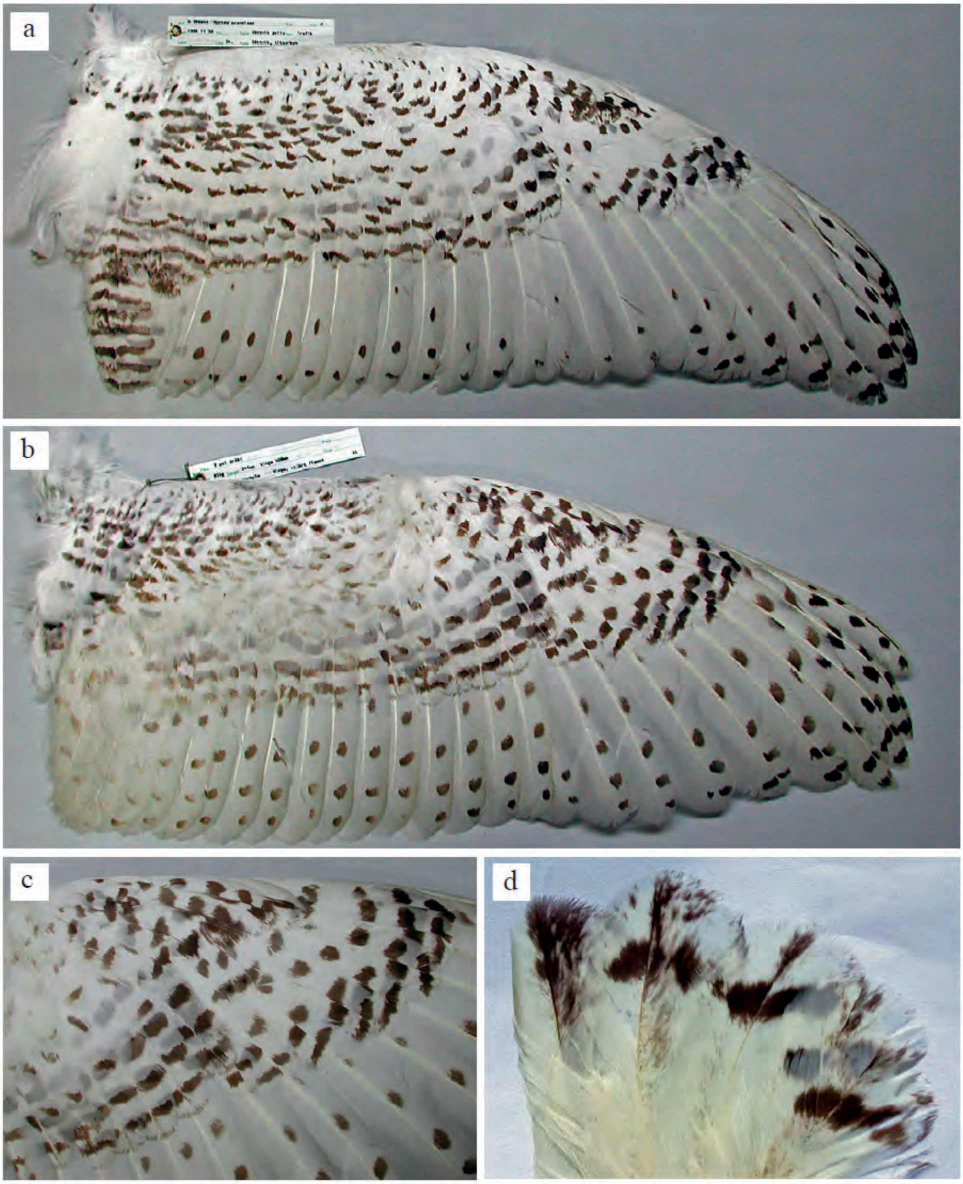
Abbreviations: J: juvenile, N: new, non-juvenile feather. Numbers indicate feathers of same generation; 1 older than 2. P: primary. HZM: Zoological Museum, Helsinki; KZM: Zoological Museum, Copenhagen; NRM: Natural History Museum Stockholm; SMS.: Smithsonian Institution, Washington, ZMO: Zoological Museum, Oslo.



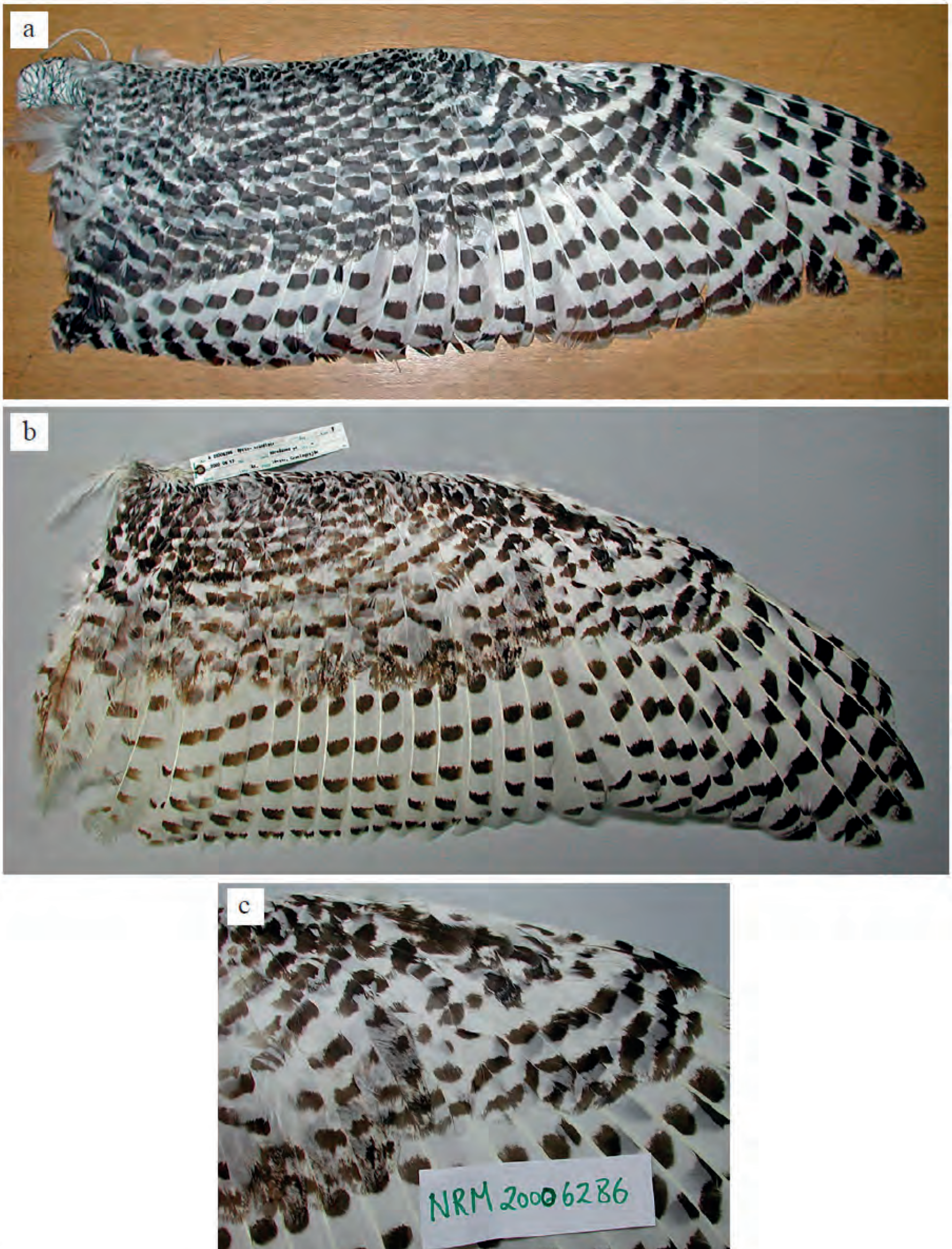
Appendix 1.1. Outer primaries of four juvenile (1Ca-2Cs) male Snowy Owls, showing variation in number and extension of dark bands and mottling. Specimen numbers: HZM8621 (a), KZM67149 (b), SMS 239186 (c) and KZM 39515 (d).



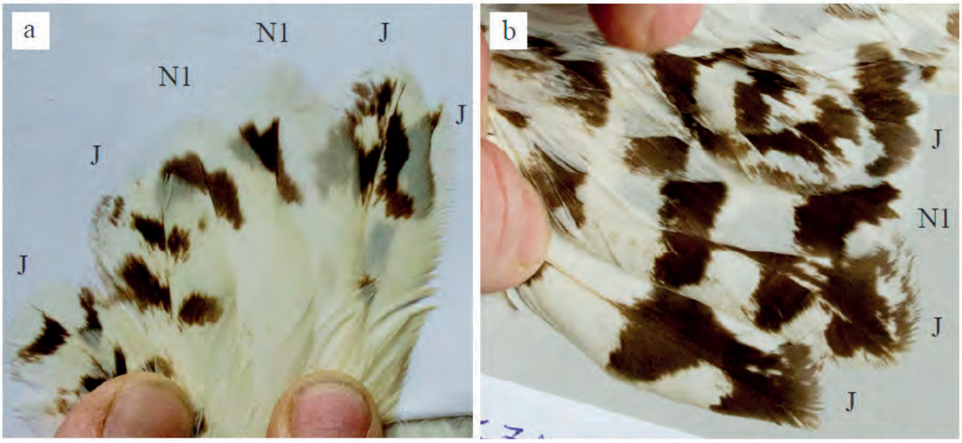
Appendix 1.2. Outer primaries of three juvenile (1Ca-2Cs) female Snowy Owls, showing variation in mottling. Specimen numbers: KZM39454 (a), KZM39532 (b), KZM39473 (c).



Appendix 1.3. Extended wings of two slightly mottled juvenile males from November (a) and July (b), showing difference in bleach and abrasion on tertials and inner secondaries before onset of first moult M1, and close up of primary (c) and secondary (d) coverts of two juvenile males, showing mottling on coverts. Specimen numbers: NRM996648 (a), NRM20006304 (b, c) and KZM39488 (d).



Appendix 1.4. Extended wings of two juvenile female Snowy Owls from January (a) and June (b), showing difference in bleach and abrasion on tertials and inner secondaries before onset of first moult M1, and close up of coverts of the June bird, showing marked mottling especially on secondary coverts (c). Specimen numbers: HZM24740 (a) and NRM20006286 (b, c).

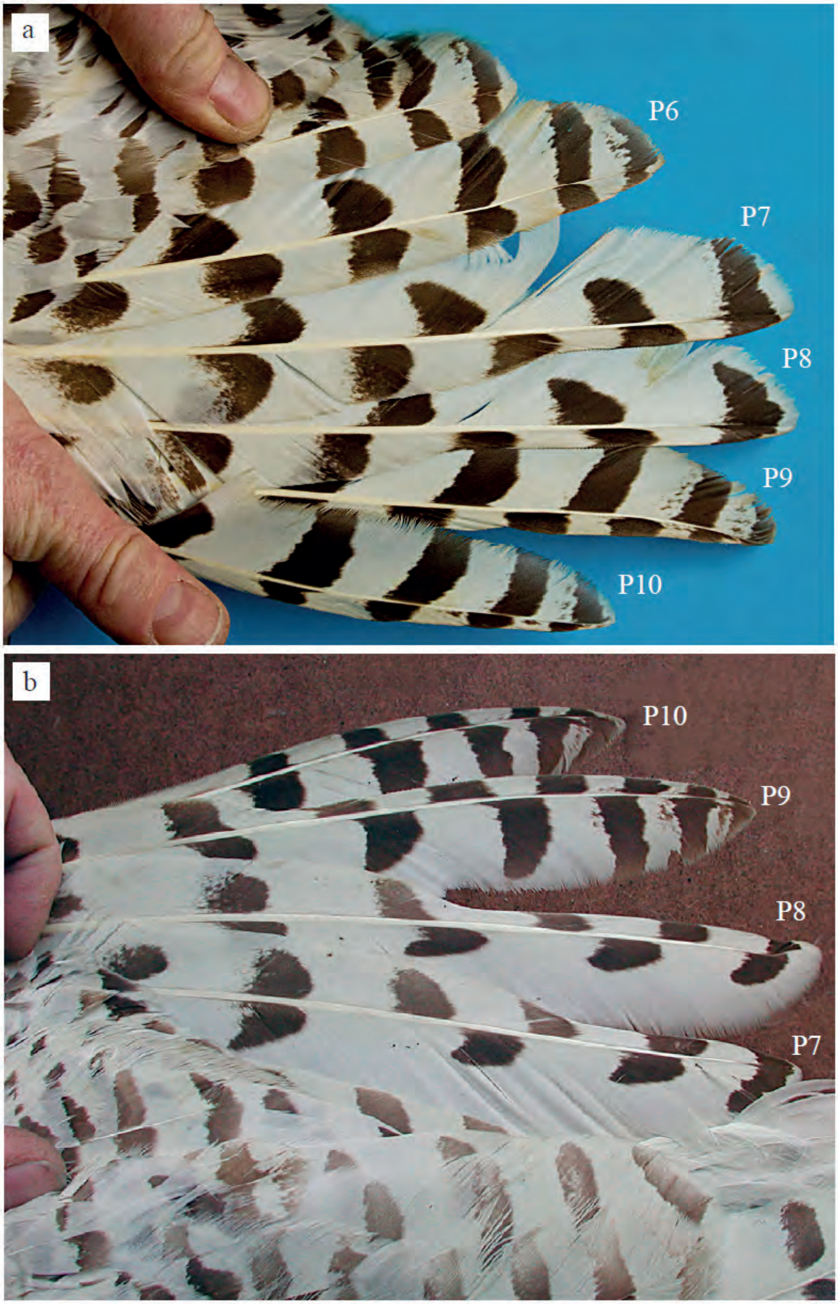


Appendix 1.5. Greater coverts of male (a) and female (b) Snowy Owls after first moult M1. J: Juvenile feather, N1: first generation of adult, non-juvenile feather. Specimen numbers: KZM39452 (a) and KZM39554 (b).

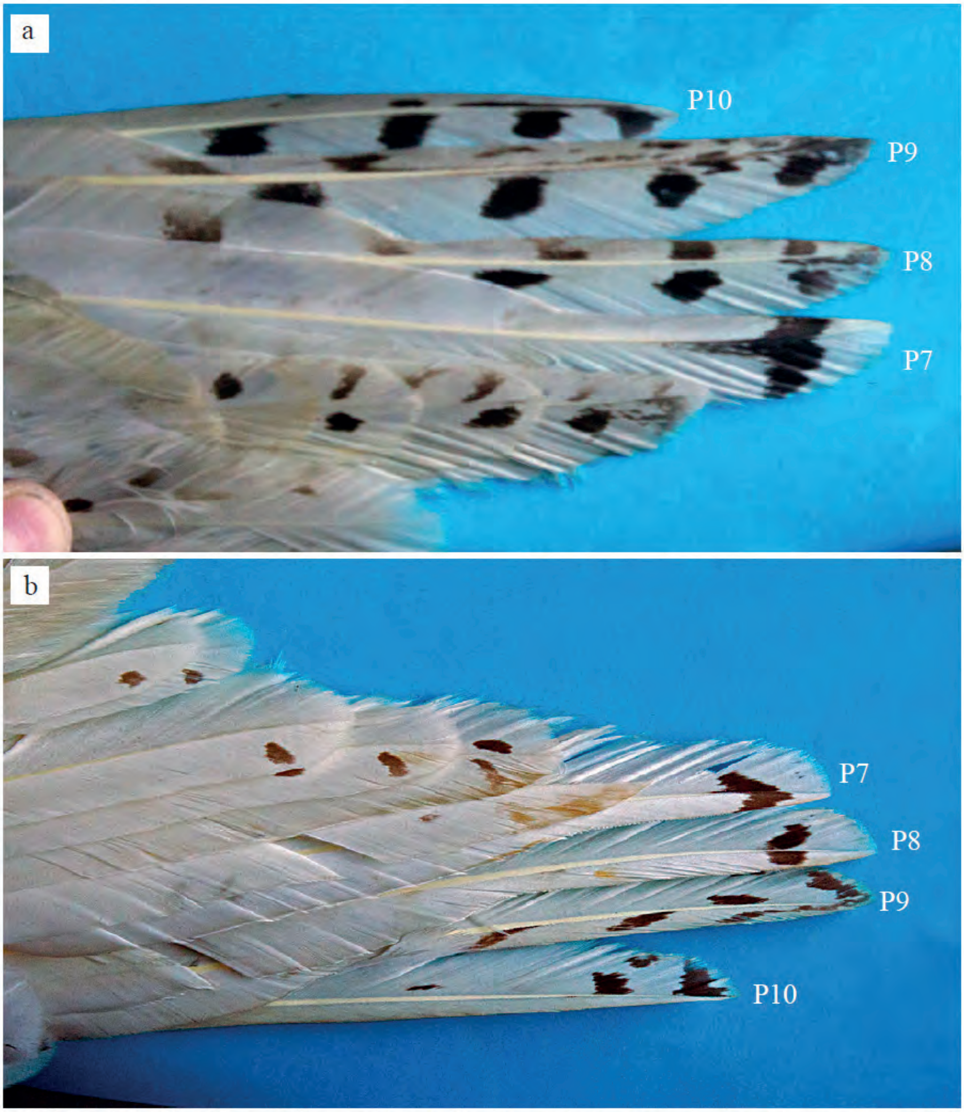
Appendix 1.6. Outer primaries of male (a) and female (b) Snowy Owls after first moult M1. J: Juvenile feather, N1: first generation of adult, non-juvenile feather. Specimen numbers: KZM39452 (a) and KZM39554 (b).

Appendix 1.7. Wing of 2Cs female from 28. January, with primaries P6-P10 showing lack of white outer fringe. Note also mottling between the outer dark bands on primaries P5-9. Specimen number: SMS 614342.

Appendix 1.8. Primaries P5-10 of a 3Cs female January. P7 is not easy to distinguish as N1 compared with the other primaries. However the terminal dark band is broader than on P6 and P8. Also P7 is fresh, while P6 and P8 are abraded and bleached. Because P7 is the most exposed primary of the wing, it should have been even more bleached than its neighbours if it belonged to the same generation.

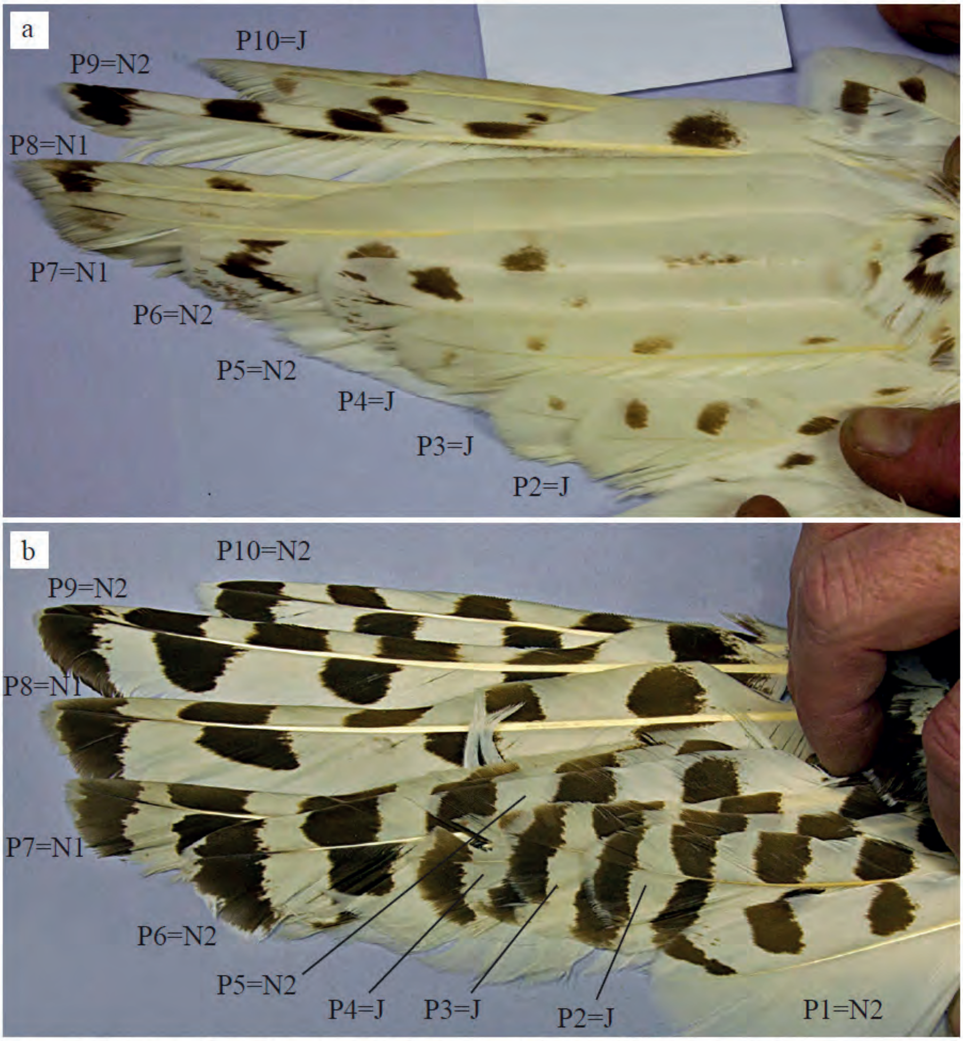


Appendix 1.9. Primaries of females after their second moult M2, 3Ca female from 5. September (a) and 4Cs female from March (b). P7 and P8 are non-juvenile, fresh feathers with marked outer, white fringe and shortened dark crossbands on inner vanes. Specimen numbers: KZM39546 (a) and KZM 39568 (b).



Appendix 1.10. Primaries of males after their second moult M2, both from October. In (a) only P7 is of N1 generation, in (b) both P7 and P8 are N1 generation. Note the broad terminal white fringe on the new N1 feathers as opposed to the neighbouring juvenile primaries. Specimen numbers: KZM30742 (a) and KZM39441 (b).

Appendix 1.11. Primaries of a 3Ca male after second moult M2, 11. November. P7 and P8 are new, N1 feathers, but may by themselves appear juvenile because of slight mottling. However compared to P6 and P9-10, they clearly stand out as non-juvenile. Specimen number: KZM39513.



Appendix 1.12. Primaries of male (a) and female (b) after third wing feather moult M3. J: juvenile, N1: first generation adult and, N2: second generation adult feather. In the male P1 is hidden, and in the female the tip of P5 is broken. Specimen number: SMS 202672 (a) and SMS 479307 (b).

Appendix 2. Individual data

Appendix 2 Moult pattern of Snowy Owl skins with recognisable juvenile feathers in the wings, from collections at Copenhagen Zoological Museum (KZM), Natural History Museum Stockholm (NRM), Smithsonian Washington (SMS) and Natural History Museum Oslo (ZMO). J: juvenile, N: New, non-juvenile feather, O: old, ?: undefined status, -: missing feather (moulted), R, L: right/left wing. Numbers indicate feathers of same generation; 1 older than 2. a, b, c: feathers of same generation/colour pattern.

Catalogue no	Sex	Date (ddmm)	Primaries										Secondaries																	
			10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
First moult M1																														
ZMO 2604	M	1608	J	J	J	n	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	R	
			J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	L	
NRM 568863	M	0211	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	R=L	
KZM 39452	M	0401	J	J	N	N	J	J	J	J	J	-?	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	R	
			J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	L	
KZM 39561	M	2501	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	N	R=L	
KZM 39563	F	0607	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	-	-	R=L	
KZM 39502	F	1407	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	n	n	n	R	
			J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	n	n	n	n	L	
KZM 39542	F	1507	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	-	R=L	
SMS 237389	F	1110	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	J	N	N	R=L	
ZMO 2628	F	1410	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	-	-	R=L	
NRM 926459	F	1111	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	-	R=L	1)
KZM 39485	F	2611	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	R=L	
NRM 568836	F	1612	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	-	R=L	1)
SMS 195604	F	1812	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	R=L	
KZM 39508	F	Aut.	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	R=L	
KZM 39565	F	1211	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	R=L	
NRM 611147	F	1311	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	-	R=L	1)
KZM 39480	F	0112	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	R=L	
KZM 39554	F	0312	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	R=L	
ZMO 2606	F	0512	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	R	
			J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	L	
ZMO 2608	F	1512	-	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	R	
			J	J	J	N	J	J	J	J	J	-	J	J	J	J	-	J	J	J	J	J	J	N	N	N	N	N	L	2)

NRM 866747	F	1812	J	N	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	-	L	1)
ZMO 11576	F	Jan.	J	J	J	N-	J	J	J	J	J	-	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	R	3)
			J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	-	L	
KZM 39525	F	2101	J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	-	R	
			J	J	J	N	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	L	
Second moult M2																														
SMS 81397	M	2708	J	J	n	N	J	J	J	J	J	J	O	n	O	O	n	O	O	O	O	n	n	n	n	N1	N1	N1	R	
			J	J	n	N	J	J	J	J	J	J	O	n	O	O	n	O	O	O	n	n	n	n	N2	N1	N1	N1	L	
KZM 30742	M	2010	J	J	J	N	J	J	J	J	J	J	O	O	O	O	N	N	O	O	O	O	O	O	N	N	N	O	R	
			J	J	J	J	J	J	J	J	J	J	O	O	O	O	O	O	O	O	O	O	O	O	N	N	N	N	L	
KZM 39441	M	2510	J	J	J	N	J	J	J	J	J	J	N	O	O	O	O	O	O	O	O	O	O	O	N	N	N	N	R	
			J	J	N	N	J	J	J	J	J	J	N	O	O	O	O	O	O	O	O	O	O	O	N	N	N	N	L	
KZM 39513	M	1111	J	J	N	N	J	J	J	J	J	J	O	N	N	O	N	O	O	O	N	N	N	N	N	N	N	N	R=L	
NRM 568881	M	1211	J	J	N	N	J	J	J	J	J	J	O	N	O	O	N	O	O	O	O	O	N	N	N	N	N	N	R=L	
KZM 39461	M	2011	J	J	N	N	J	J	J	J	J	J	N	N	O	O	N	O	O	O	O	N	N	N	N	N	N	N	R=L	
SMS 190690	M	3012	J	J	n	N	J	J	J	J	J	J	O	nl	O	O	O	N1	N?	N?	N?	N?	N?	N?	O	O	O	O	R=L	4)
ZMO 2620	M	1202	J	J	N	N	J	J	J	J	J	J	N	N	O	O	N	O	O	O	O	O	O	N	N	N	N1	N1	R	
			J	J	N	N	J	J	J	J	J	J	N	O	O	N	O	O	O	O	N	N	N	N	N1	N1	-	-	L	
NRM 568874	M	2404	J	J	N	N	J	J	J	J	J	J	O	N	N	O	N	O	O	O	O	O	N	N	N	N	N	-	L	1)
KZM 39448	M	2805	J	N	N	N	J	J	J	J	J	J	N	O	N	O	O	O	O	O	N	N	N	N	N	N	O	O	R	
			J	N	N	N	J	J	J	J	J	J	N	O	O	O	O	O	O	N	N	N	N	N	N	N	N	O	L	
KZM 39546	F	0509	J	J	N	N	J	J	J	J	J	J	O	N	N	O	N	O	O	O	N	N	N	N	N	N	N	N	R=L	
SMS 589856	F	1511	J	J	N	N	J	J	J	J	J	J	N	N	O	N	O	O	O	O	O	O	N	N	N	N	N	N	R	
			J	J	N	N	J	J	J	J	J	J	N	N	O	O	N	O	O	O	O	N	N	N	N	N	N	N	L	
SMS 531718	F	1911	J	J	N	N	J	J	J	J	J	J	N	O	N	O	N	O	O	O	O	O	N	N	N	N	N	N	R	
			J	J	N	N	J	J	J	J	J	J	N	N	O	O	N	O	O	O	O	N	N	N	N	N	N	N	L	
KZM 39446	F	2702	J	J	J	N	J	J	J	J	J	J	O	N	O	O	N	O	O	O	N	N	N	N	N	N	N	O	R	
			J	J	J	N	J	J	J	J	J	J	O	N	O	O	N	N	O	O	N	N	N	N	N	N	N	O	L	
NRM 568829	F	0002	J	N	N	O	N	J	J	J	J	J	J	N	J	J	N	N	J	N	N	N+	O	O	O	O	O	-	R=L	1)
KZM 39568	F	0003	J	J	N	N	J	J	J	J	J	J	O	N	O	O	N	O	O	O	O	N	N	N	N	N	N	N-	R	
			J	J	N	N	J	J	J	J	J	J	O	N	N	O	N	N	O	O	O	N	N	N	N	N	N	N-	L	
KZM 39501	F	0904	J	J	N	N	J	J	J	J	J	J	N	O	O	O	O	O	O	O	-?	N	N	N	N	N	N1	N1	R	

			J	J	N	N	J	J	J	J	J	J	N	N	O	O	N	O	O	O	O	N	N	N	N	N	N1	N1	L	
NRM 568865	F	0205	J	J	J	N	J	J	J	J	J	J	N	O	O	O	N	O	O	O	O	O	N	N	N	N	N	N/O	R=L	
SMS 256906	F	2505	J	N	N	N	J	J	J	J	J	J	N	N	O	N	O	O	O	O	N	N	N	N	N	N/O	O	O	R	4)
			J	N	N	N	J	J	J	J	J	J	N	N	N	O	N	O	O	O	O	N	N	N	N	N	N/O	O	L	
Third moult M3																														
SMS 589854	M	1107	O	O	O	O	n	n	J	J	J	n	N1	O	n*	O	O	O	O	O	X	X	X	N1	O	O	-	n	R	
			O	O	O	O	n	n	J	J	J	J	N1	O	n*	O	O	O	O	O	-	n	N1	N1	O	O	n	n	L	
SMS 325409	M	1809	N2	N	N	N1	N	N	J	J	J	N2	N	O	N	N	O	O	N2	N1	O	n	N	N	N	N	N	N	L	5)
KZM 39537	M	Aut.	J	N	O	O	N	J	J	J	J	N	N	O	N	O	O	N	N	N	O	O	O	N	N	N	N	N	R	
			J	N	N	O	N	J	J	J	J	N	N	N	O	N	O	O	N	N	N	N	O	O	N	N	N	N	L	
SMS 241221	M	1302	J	N2	N1	N1	N2	J	J	J	J	J	N	N*	N*	O	N	O	O	O	N	N*	N	N*	N1	N1	N1	N1	R	6)
			J	N	N	N	N2	J	J	J	J	J	N	N*	O	O	N	O	O	O	N*	N*	N*	N*	N1	N1	N1	N1	L	
KZM 39507	M	Spring	J	N	O	O	O	N	J	J	J	J	O	O	O	O	O	O	O	O	O	O	O	O	O	O	N	N	R	
			J	N	N	O	O	N	J	J	J	J	O	O	O	O	O	O	O	O	O	O	O	O	O	N	N	N	L	
SMS 202672	M	Sum.	J	N2	N1	N1	N2	N2	J	N	N	N	N2	N1	N2	N2	O	N2	N1	N2	O	O	O	O	O	O	N	N	R	
			J	N2	N1	N1	N2	N2	J	J	J	N2	N2	N1	N2	O	O	N2	N1	N2	N1	O	O	O	O	O	N	N	L	
KZM 39505	F	1501	J	N2	N2	N1	N2	J	J	J	J	N	N	N	N	O1	O	N	N	O1	O	N	N	O	O	N	N	N	R	
			J	N2	N2	N1	N2	J	J	J	J	N	O	N	N	O1	O	N	N	N	N	N	N	O1	O1	O1	N	N	L	
SMS 479307	F	0704	N	N2	N1	N1	N2	N2	J	J	J	J	N	N	N	N	O	N	N	N	N1	O	O	O	N	N	O	O	R	
			N	N2	N1	N1	N2	N2	J	J	J	N2	N	N	N	N	O	N	N	N	N	O	O	O	N	N	O	O	L	
KZM 39459	F	2806	J	N	N	O	N	N	J	J	J	J	O	N	N	N	O	N	N	N	O	O	O	O	N	N	O	O	R	
			J	N	N	O	N	J	J	J	J	J	O	N	N	N	O	N	N	N	O	O	O	O	N	N	O	O	L	
KZM 39477	F	1110	N	N	N1	N1	N	N	J	J	J	N	N	N	N	N	N	N	N	N	N	N	O	O	N	O	O	O	R	
			N	N	N1	N1	N	N	?	J	N	N	N	N	N	N	N	O	N	N	N	N	O	N	N	N	N	N	L	
ZMO 17464	F	0000	N2	N2	N2	N1	N2	N2	J	J	J	N	N	O	O	N	O	O	N	O	O	N	N	O	O	N	O	O	R	
			N2	N2	N2	N1	N2	N2	J	J	J	N	Na	Ob	Na	Ob	Ob	Ob	Nc	Nc	Nc	Nc	Nd	Nd	O	N	N	N	L	

1) Bird has probably only 15 secondaries.
2) P10R and P1L lost due to gunshot, S5L probably removed by humans from dead bird.
3) P7R probably removed by humans from dead bird. Corresponding greater covert 7 new, adult. S16L probably also removed by humans.
4) Bird from zoological garden/captivity.
5) Right wing soiled, impossible to distinguish feather generations.
6) N*: non-juvenile feathers white without dark spots.

PAPER III

Releasing a satellite-tagged female Great Grey Owl in Torneo, Finland, July 1, 2019. Photo: Matti Suopajärvi.

Studying moult and flight feathers on a 5CY+ female Great Grey Owl, Løten, Hedmark June 18, 2013. Photo: Kjell Isaksen.

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IDENTIFYING INDIVIDUAL GREAT GRAY OWLS (*STRIX NEBULOSA*) AND SNOWY OWLS (*BUBO SCANDIACUS*) USING WING FEATHER BAR PATTERNS

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Abstract.—Bar patterns on flight feathers of Great Gray Owls (*Strix nebulosa*) and Snowy Owls (*Bubo scandiacus*) are variable, and can be used to recognize individual birds. Here I illustrate a method for taking photos of wings of captured owls and describe a way to arrange images of flying birds for comparison with photos of birds in flight or in the hand. I report four examples. First, two Great Gray Owls photographed in flight on different days at the same site were shown to be the same individual, but differed from a dead owl found at that location a month later. Second, I compared eight photographs of wintering Snowy Owls in flight in Saskatchewan and determined that they portrayed seven different owls. Third, I examined photos of breeding male first-year Great Gray Owls at neighboring nest sites and established that they were different birds. Finally, I compared photos of breeding female Great Gray Owls at the same nest site in 2011 and 2013, and determined that they showed two individuals. I suggest that such photography may be used as a tool to census populations of Great Gray Owls and Snowy Owls.

Key Words: *Great Gray Owl*; Strix nebulosa; *Snowy Owl*; Bubo scandiacus; *digital photography*; *individual identification*; *plumage.*

IDENTIFICACIÓN DE INDIVIDUOS DE *STRIX NEBULOSA* Y *BUBO SCANDIACUS* UTILIZANDO LOS PATRONES DE BARRAS DE LAS PLUMAS DEL ALA

Resumen.—Los patrones de barras de las plumas de vuelo de *Strix nebulosa* y *Bubo scandiacus* son variables y pueden ser utilizados para reconocer aves individualmente. En este trabajo, presento un método de toma de fotografías de las alas de los búhos capturados y describo una manera de organizar las imágenes de las aves en vuelo para compararlas con las fotos de aves en vuelo o capturadas, por medio de cuatro ejemplos. Primero, dos individuos de *S. nebulosa* fotografiados en vuelo en diferentes días en el mismo sitio demostraron ser el mismo individuo, pero difirieron de un búho muerto encontrado en esa ubicación un mes después. Segundo, comparé ocho fotografías de individuos invernantes de *B. scandiacus* en vuelo en Saskatchewan y determiné que correspondían a siete búhos diferentes. Tercero, examiné fotos de un macho reproductivo del primer año de *S. nebulosa* en lugares de nidificación vecinos y comprobé que eran aves diferentes. Finalmente, comparé fotos de una hembra reproductora de *S. nebulosa* en el mismo lugar de nidificación en 2011 y 2013 y determiné que pertenecían a dos individuos. Sugiero que este tipo de fotografías pueden ser utilizados como una herramienta para censar poblaciones de *S. nebulosa* y *B. scandiacus.*

[Traducción del equipo editorial]

Large mammals that are easily detected and observed in the wild have long been individually identified based on unique physical traits. For example, individuals can be identified by facial differences among chimpanzees (*Pan troglodytes*; van Lawick-Goodall 1971) and gorillas (*Gorilla gorilla*; Schaller 1963, Fossey 1983) as easily as among humans. Physical traits were used to distinguish individual lions (*Panthera leo*; Schaller 1972) and other big cats, sea lions (Osterrieder et al. 2015), elephants (*Loxodonta* sp.; Douglas-Hamilton and Douglas-Hamilton 1975, Moss 1988) and whales (for which notches and color patterns on fins and tails are diagnostic; Hamilton et al. 2007). Similarly,

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Scott (1966) noted that the pattern of yellow and black on the bills of Tundra Swans (*Cygnus columbianus*) was highly variable, and could serve as a clue to individual recognition. Whooper Swans (*Cygnus cygnus*), on the other hand, were not as variable as Tundra Swans, making individual recognition more difficult for this species (Brazil 1981).

Frequent encounters and familiarity with a group of birds may enhance the ability to recognize individuals by plumage, but often such recognition based on physical differences is imperfect (McLaren 1975, Harper 1982). For example, in Norway, black belly notches have been used to recognize individual Lesser White-fronted Geese (*Anser erythropus*) at a staging ground (I. Øien pers. comm), but the method is not definitive because feather patterns change from spring to autumn. Thus, only geese with very extreme patterns can be recognized from one year to the next. Because of such challenges, individual recognition of birds in the field based on plumage characters has not been applied on a larger scale to date. Based on studies of the molt patterns of Great Gray Owls (*Strix nebulosa*; Solheim 2011) and Snowy Owls (*Bubo scandiacus*; Solheim 2012), and field studies on both (Solheim et al. 2008, Jacobsen et al. 2009, Solheim 2010, Berg et al. 2011, Solheim 2012, 2013), I have used modern digital photography and bar patterns on flight feathers as a tool to recognize individual birds of these two species. Here, I describe how to photograph captured and free-ranging owls, and how to distinguish differences in the size, shape, and color of wing feather bars. I present four examples in which this method was used to identify individuals based on photographs taken of birds in the wild.

Methods

Photography Equipment. Any digital camera can be used to photograph birds in the hand provided it can capture the length of the entire wing on the image. I used a 35–50 mm lens and typically photographed the wing with a contrasting background (dark for Snowy Owls, light for Great Gray Owls). When possible, I avoided using a flash because it can distort the color contrasts between new and old feathers. When photographing owls, I used Canon D7 and D7 MkII cameras, with a Canon 500 mm 4.0 L IS USM lens (and sometimes a Canon 1.4 extender) or Canon 100–400 IS USM lens. For this type of photography, I prefer cameras that allow high ISO values, because shutter speeds of 1/1000 sec or faster should be used in dim light. Cameras should have at least 20 mega-pixels to allow cropping images of owls photographed at long ranges. Many modern cameras of several brands also have GPS units, allowing each image to be stored with exact location data.

I typically photographed owls in RAW mode for the best opportunity to enhance images shot in dim light. I digitally enhanced most photos to give the best comparison of feather barring among individual owls. I used Photoshop CS5 and CS6 software programs to enhance sharpness and contrast.

Taking Images of Captured Birds. When I captured an owl, I photographed each wing to show all primaries and secondaries and their bar patterns. This was preferably done with another researcher, so that one person held the owl and stretched out its wings one at a time while the other photographed. The primaries were well extended and the feathers arranged so they were all straight and showed the respective upper parts of the outer vanes (Fig. 1). The outermost primaries P9 and P10 were easily covered by the longer P8 and P7, so great care was taken to spread out these outer primaries. Birds as large as Snowy and Great Gray owls often tilted so the lower end (edge) of a wing bent away from the photographer; however, I took photos perpendicular to the wing plane (Fig. 2).

When photographing without help, I placed the bird at ground level and pulled out one wing at a time onto the ground. While holding the bird's feet with one hand, I used the other to operate a compact camera. However, this was not easy and rarely provided optimal images. As an alternative, I sometimes placed the camera on a tripod, set the shutter at 10-sec delay, and held the bird with one outstretched wing in front of the camera.

Taking Images of Flying Birds. Because free-ranging birds were photographed opportunistically, it was impossible for me to take images from the same angle at all times, as when photographing a bird in the hand. Even with the most advanced camera, it was challenging to photograph the upper wing surface of a flying owl to match against wing photos in a databank. However, I found that images of the underside of the wing sometimes also worked well, when light from above shone through the wing and made it possible to see barring from the underside of the feathers (Fig. 8, 10). However, underside images presented a smaller area of the wing for comparison than upper-side images, as only the part of flight feathers not overlapping with neighboring feathers showed clear views of the

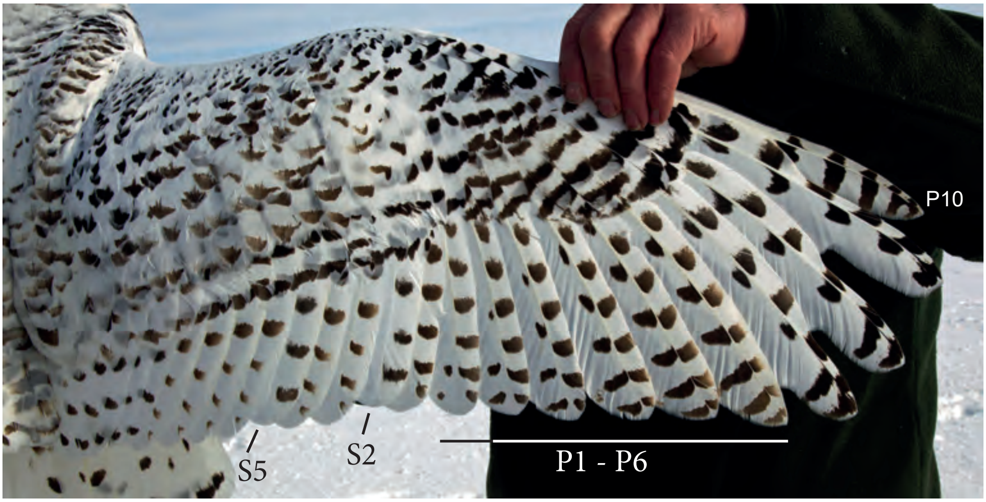

Figure 1. Wing of female Snowy Owl stretched out with outer vane of both primaries and secondaries visible. Primaries P1–P6 and P10, and secondaries S1, S3–S4, and S6–S9 are juvenile. Note that the dark bars on the inner vane are longer on juvenile than on adult primaries. Note also how the outer bars on P7 connect in a zig-zag pattern toward the rachis as opposed to the outer bars on juvenile feathers P5 and P6. On juvenile secondaries, there are (at least) four dark bars visible on the outer vane, whereas on the adult secondaries only three bars can be seen.

barring patterns. On an upper-side view, crossbar patterns showed clearly on the outer vane of each flight feather, although each overlapped with inner vanes of neighboring feathers.

The best opportunity for taking a good photo of the wing pattern of a flying owl was when the owl passed above me. These opportunities were infrequent for the wary Snowy Owl, but more common for the bolder Great Gray Owl, which sometimes flew directly overhead or approached closely to protect its nest or offspring. I shot images at the greatest number of frames per second as owls flew overhead, to maximize the opportunity to produce some usable images.

Comparing Patterns of Barring on Wing Feathers. The primaries usually gave the best opportunities for comparing bar patterns, but the secondaries sometimes added useful information. In both feather tracts, it was helpful to distinguish the pattern of old and new feathers based on the molt generations (Fig. 1). Birds in their first year (first calendar year autumn and second calendar year spring), before their first wing feather molt, did not have feathers of varying color and wear. Both owl species started their first wing molt with the innermost secondaries, and one to three of the longest primaries (Solheim 2011, 2012). After this stage, wings usually displayed feathers of different age and wear. The order of new and old wing feathers was helpful for recognizing an individual bird, and sometimes helped to separate individuals within the same molt cycle (from autumn year X to spring year X+1).

When I compared an image of the underside of a wing with an upper-side image of the same wing from another bird or situation, I used Photoshop to mirror one of the images for easier comparison of the patterns of the dark spots and bars on the

Figure 2. Owl wing being photographed in the correct manner.

Figure 3. Right wing of female Great Gray Owl banded on 18 June 2013 and recaptured on 27 May 2014. Primaries P2 and P5 were molted during summer 2013. Circles outline where differences in bar patterns in this case are most easily seen. Note differences in how bars on outer and inner vane connect toward the rachis. Feathers not molted are linked with lines. Note that the image from 2014 is not optimal, because bar patterns of the outer primaries P8–P10 cannot be seen properly.

feathers. To separate individuals, I needed only a single difference in the bar pattern on one feather. To conclude that two images portrayed the same individual, I matched up at least several bar patterns on more than one feather, especially those markings of an unusual size or shape. I looked for clues, such as the thickness of bars, distance between bars, the form of the edge of a dark bar toward light areas, and differences in how bars from the outer and inner vanes aligned toward the rachis. Within one molt cycle (from autumn year X to spring year X+1), each individual had the same bar pattern, and any feather in a wing image could be compared with the same feather of a different wing image. Because each wing feather is retained for 2–4 yr in Snowy or Great Gray owls before it is molted (R. Solheim, unpubl. data), it was sometimes possible for me to recognize an individual from year X up to year X+3 or in rare cases up to year X+4. Fresh feathers in year X were compared with worn feathers in the same position in a later year (see Fig. 3).

RESULTS

I photographed and compared bar patterns of Great Gray Owls at the same locality on different dates, female Snowy Owls on wintering grounds, subadult Great Gray Owl males at neighboring nest sites, and female Great Gray Owls at the same nest site over a 2-yr period. Below, I describe how I used wing photography to answer questions about individual owl identities in the field.

Figure 4. Great Gray Owl photographed on different dates by H. Sørhuus (left) and T. Kolaas (right) in Levanger, North Trøndelag, Norway, April 2009. The first clue to similarities of these two images is the difference in molt on the left and right wings. On the left wing, only P5 is a non-juvenile primary, while on the right wing the three primaries P4–P6 have been molted. The rest of the primaries have light tips and a narrow, outer dark bar, diagnostic of juvenile flight feathers on Great Gray Owls (Solheim 2011).

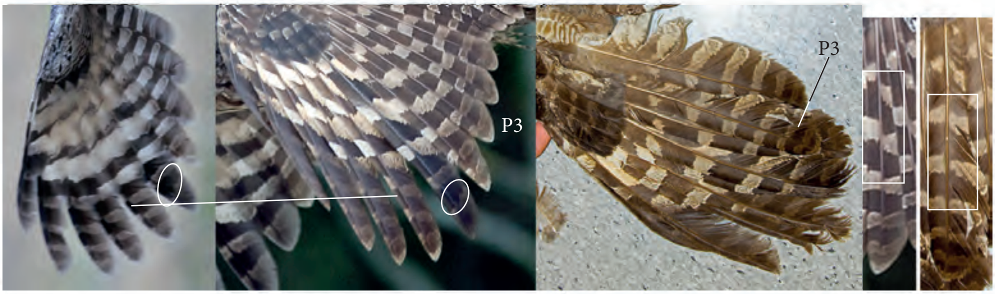

Figure 5. Primaries of the left wings of the two flying birds from Figure 4, and the wing of a Great Gray Owl found dead in Levanger, 20 May 2009. On the wing images, the most striking similarities are the outer edge on the dark bar on the inner vane of P5 (white circle), and the pattern of bars toward the rachis on P6 (white line). The bar edges are also similar. Primary P3 from the live (left) and dead (right) birds are aligned for easier comparison at right. The bar section that differs the most is outlined.

Great Gray Owls at the Same Locality on Different Dates. In mid-central Norway, two researchers/photographers shot images of flying Great Gray Owls at different dates during April 2009 (Fig. 4). Both images of the flying owls showed P5 on the left wing was a dark, adult feather, whereas the other primaries were juvenile; thus, both images were of owls after the first wing feather molt. The molt was asymmetric, with the three primaries P4–P6 molted on the right wing. The asymmetry suggested that the images might show the same individual. By mirroring the left wing primaries on the bird flying toward the photographer, I easily compared the bar patterns of the primaries. Shape and alignment of the bars on several of the primaries showed that these images portrayed the same individual (Fig. 5). On 20 May 2009, a Great Gray Owl was found dead in the same region and brought to the Natural History

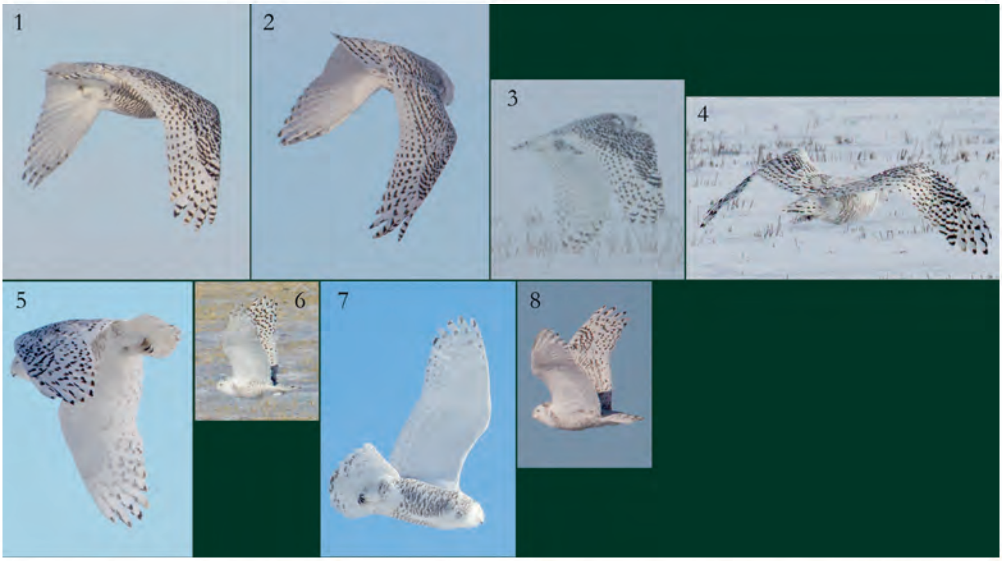

Figure 6. Female Snowy Owls photographed in southern Saskatchewan on 5 February (numbers 1 and 2), 15 February (numbers 3 and 4), 17 February (numbers 5 and 6) and 18 February (numbers 7 and 8), 2014.

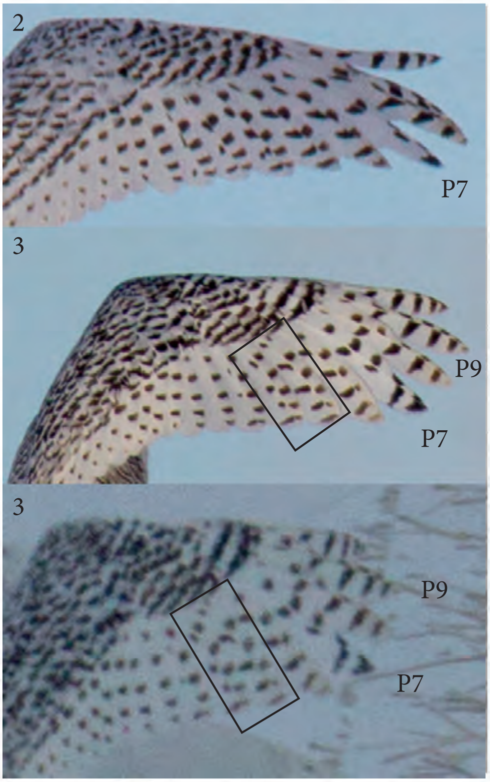

Figure 7. The right wings of the three first females shown in Figure 6. Because all images show birds with juvenile P8 – P10 (Solheim 2012), and adult P7, they are obvious candidates for comparison. For bird number 1 and number 2, it is sufficient to note the differences of the bar patterns on primary P7 to see that these are different individuals. On female 1, the second bar on P7 crosses over the entire width of the inner vane, whereas on female 2, this bar is a thin line toward the rachis. Although image 3 was taken under difficult light conditions at long distance and is blurred when magnified, it is possible to compare the shape of the bars with those on the other images. The pattern of the bars on P7 is similar to the pattern on P7 on image 1. Similarly, the bars on P9, which meet in a zig-zag pattern toward the rachis (as opposed to the bars on P10), are similar in both images 1 and 3. The arrangement of the bars on P4 and P5 within the squares is very irregular and distinctive, and similar on the two images.

Museum in Trondheim. The dead owl too had molted P5 on its left wing. When I compared the primary P3 on the photos of the flying owls and the dead owl, I found they differed markedly in how the three outermost dark bars met toward the rachis (Fig. 5). The dead owl was definitively not the one that was encountered earlier by the two photographers.

Female Snowy Owls on Wintering Grounds. During February 2014, I photographed eight flying female Snowy Owls in southern Saskatchewan on their wintering grounds (Fig. 6). Enlargement of the images of the wings of the birds demonstrated that images 1 and 3 portrayed the same individual, whereas the other birds were different individuals, based on differences of the primary P7 alone (Fig. 7).

Subadult Breeding Great Gray Owl Males at Neighboring Nest Sites. In 2014, I found two nests of Great Gray Owls in southeastern Norway that were spaced 810 m apart. At both nests, the male was a first-year bird, as determined by capture at one site and good wing photos of the flying male at the other site (Fig. 8). Because only five of 64 breeding Great Gray Owls that I aged were first-year birds in 2014 (R. Solheim unpubl. data), there was a possibility that these two neighboring nests were attended by a bigamist male. I compared the wing photos of the captured bird and the flying bird (Fig. 9). The dark bars on the inner vane of P2–P4 were wider than the light areas between them on one bird, but similar in width on the other bird. On P4 there was a dark area along the rachis combining bars 3 and 4 on inner vane on one bird, visibly different from the same area on P4 on the other individual. Thus, I determined that they were different individuals.

Female Great Gray Owls at the Same Nest at a 2-yr Interval. On 28 May 2011, I caught, banded, and photographed a female Great Gray Owl nesting in an old Northern Goshawk (*Accipiter gentilis*) stick nest. This bird was a first-year breeder, as all its wing feathers were juvenile. Two years later, the nest was once again occupied by Great Gray Owls. Although I was unable to catch this female, good wing images (Fig. 10) revealed that she had molted twice (Solheim 2011) and was thus hatched in 2010. She was thus the same age as the female that bred at the same location in 2011. Because the wing of the 2013 bird had retained several juvenile feathers, I compared these with the same feathers on the female from 2011. The outermost crossbar on P1 and P2 produced the best images, and clearly differed between individuals (Fig. 11), demonstrating that the female in 2013 was not the same bird as in 2011.

Figure 8. Breeding juvenile male Great Gray Owls encountered at two nest sites 810 m apart on 6 June 2014. The square marks the section of the primaries that presents the best area to compare bar patterns of primaries with those on the outstretched wing of the captured male.

DISCUSSION

Photos of the outstretched wings of Great Gray and Snowy owls can be used to identify individuals based on ages of molted feathers and barring or spot patterns on the feathers. For Snowy Owls, particularly females, the dark spots and bars of adult primaries usually show more variation across individuals than do the juvenile feathers (R. Solheim unpubl. data). However, old Snowy Owl males have few dark spots on their primaries, and some may lack spots altogether. This method is rarely, if ever, useful for such individuals. However, even when the patterns of color on the feathers are not distinctive, wing photos can still be used to identify raptors based on the presence of gaps in the wing or partly grown feathers during a molt sequence. Some individual raptors may have such specific barring patterns that even one molted flight feather can identify a specific bird (Selås et al. 1990).

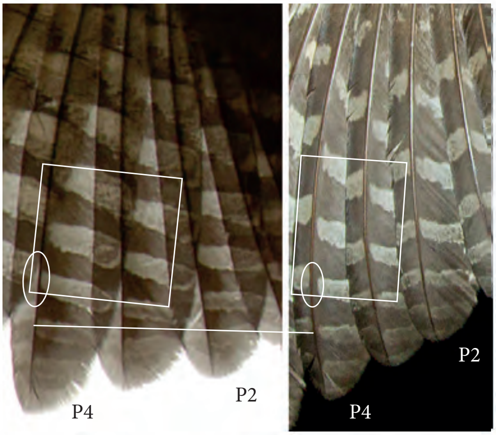

Figure 9. Primaries P2–P4 of the flying (left) and captured (right) male Great Gray Owls from Figure 8. The section from the flying bird has been mirrored. Note that the second bars from the tip of primary P4 are aligned on captured bird, as opposed to skewed toward the rachis on the flying bird (white line), that the third bar on the inner vane of the captured bird stretches in a thin line along the rachis toward the fourth bar (white circles), and that the dark bars within the white squares are conspicuously thicker than the light section between them on the captured bird, but nearly similar in thickness on the flying bird.

Although birds in hand present the best opportunities for taking good wing images, it is often impossible to catch all individuals in a small group or population. In this case, taking in-flight photos of the individuals that cannot be caught can be very useful to build a database that can be used to individually recognize all or most individuals. Even a photo taken at long range or slightly out of focus can be valuable if it shows most of the flight feathers from the upper side of the wing. A database built of wing photos can be used very efficiently within one molt cycle (late autumn to early next summer) by checking all individuals against each other. In Snowy and Great Gray owls, each flight feather is typically retained for 2–3 yr before being molted (R. Solheim unpubl. data). Some feathers may even be kept for

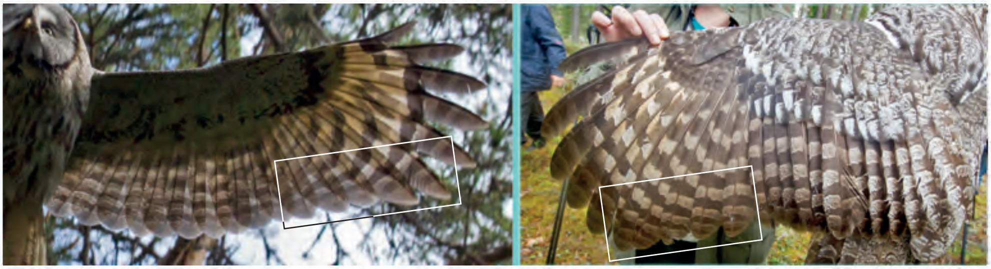

Figure 10. Underside of the left wing of the female Great Gray Owl photographed flying at a nest site on 16 June 2013 (left image), where the breeding female in 2011 was captured on 28 May (right image).

up to 4 yr. This implies that it may be possible to compare a bird with others photographed within a time period of up to 3 yr, and even maybe 4 yr.

Both Great Gray Owls and Snowy Owls occasionally have irruptive movements, during which time members of the public report frequent sightings of owls. However, such reports may overestimate owl numbers if several people see the same bird. In such cases, taking photographs of the free-ranging birds could give a more accurate estimation of the number of individuals at a specific locality. Such digital photos may also indicate the age classes involved in an invasion (Solheim 2014a).

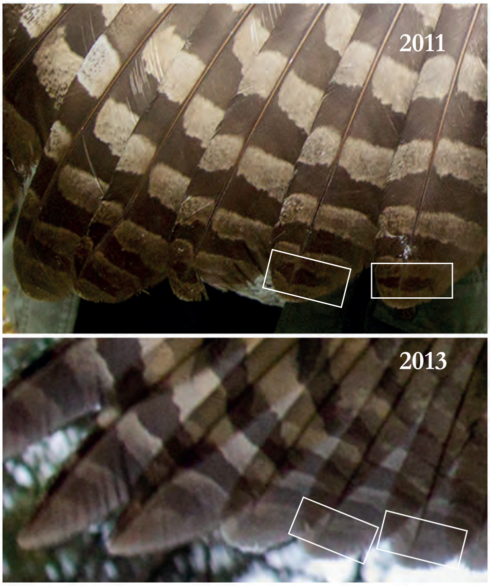

Figure 11. Primaries P1–P5 of the images in Figure 10. The section from the flying female has been mirrored (lower image). The squares outline the outermost bars on primaries P1 (right) and P2, which are still juvenile on the bird from 2013. Note that the bars on P1 are angled toward the rachis on the 2013 female, but straight on the 2011 female. On P2 the bars get markedly broader toward the rachis on the 2011 bird, whereas they are evenly broad on the 2013 bird.

By systematically photographing both wings of all individuals caught for banding, it is possible to build an archive to which other individuals may be compared. In principle, this method could be used as a capture-recapture method to estimate the size of a subpopulation, as has been done successfully for humpback whales (*Megaptera novaeangliae*, Smith et al. 1999). Images of faces of Australian sea lions (*Neophoca cinerea*) have been used with whisker spots as clues to test whether individuals can be identified by computer programs (Osterrider et al. 2015). However, the images had to be strictly standardized with regard to distance and angle of the face to work. Such software would probably only work on wing images of owls from captured birds. Wing photos of free-ranging birds come in a wide variety of angles and light conditions, and would have to be checked manually by a human observer.

I have not yet used wing images to estimate the size of any subpopulation of Great Gray or Snowy owls. However, I have captured a considerable number of adult birds of both species on breeding and wintering grounds (Solheim et al. 2007, Solheim 2014b, Jacobsen et al. 2012, Solheim et al. 2014). It takes dedication and a large effort in terms of time and resources to capture such birds, and there are always individuals that cannot be caught. Taking photos of such individuals in flight is both easier and less expensive than getting the birds in hand, and in this respect I am convinced that wing images may be applicable as a tool to census populations of Great Gray and Snowy owls.

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PAPER IV

Adult female Snowy Owl, Saskatchewan, Canada, February 17, 2016. Photo: Roar Solheim

Age and sex of Snowy Owls *Bubo scandiacus* during summer irruption on Beliy Island, Yamal in 2015.

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Key words

Bubo scandiacus, irruption, photo identification, sex and age distribution, Snowy Owl

Abstract

In early summer 2015 a superpeak of lemmings *Lemmus sibiricus* appeared on Beliy Island north of Yamal peninsula, Russia (73°19'N, 70°15'E). Considerable numbers of Snowy Owls *Bubo scandiacus* were present, possibly as a result of the abundance of lemmings. On 7, 9, 13, and 15 July a total of 69.7 km was covered on foot. Snowy owls were approached and 344 images of perching and flying birds were captured. At most 89 individual Snowy Owls were seen from one vantage point.

Images were sorted by number, time and date recorded on the image files. Images suitable to sex and age the owls were treated in Photoshop to enhance details of moult and bar patterns in wings. The birds were aged analyzing moult patterns, and individuals were recognized by bar and moult patterns in their wings.

Eleven males and 14 females were aged, of which 14 (56%) were second calendar year (2CY) birds hatched in 2014. Six owls were in their second or third wing feather moult, thus classified as 3CY-4CY birds, while only five were birds with no juvenile flight feathers left (5CY+). Several individuals only photographed perching on the ground appeared to be juvenile 2CY birds, but these were not included in the sample due to lower certainty of identifying individuals and aging perched birds from images. Although two nesting pairs were recorded, the majority of the Snowy Owls on Beliy Island in July 2015 were young, presumably non-breeding birds.

This study shows that photographying as many Snowy Owls as possible during an irruption may reveal the age and sex distribution of the birds present.

Introduction

Snowy Owls *Bubo scandiacus* have a circumpolar distribution, and can be found in the Arctic of Eurasia and North America as far north as 82ºN and south to around 60ºN (Portenko 1972). They are known to appear in great numbers at irregular intervals both on breeding grounds in summer, and on winter staging grounds (Portenko 1972). The international Snowy Owl Working Group (ISOWG) recognizes that the total world population of Snowy Owls may be far smaller than formerly believed, as indicated by DNA studies (Marthinsen et al. 2008), satellite tracking results (Therrien et al. 2008, Solheim et al. 2008, Jacobsen et al. 2009, Solheim et al. 2014) and also as proposed by Potapov & Sale (2012).

In North America Snowy Owls regularly migrate south during winter to prairie landscapes in Canada and the US, but with great fluctuations in the number of birds (Kerlinger et al. 1985, Smith 1997). When large numbers of birds appear, they are often mostly juveniles from last summer´s breeding in the Arctic (Holt et al. 2015). However, also adult, older birds may appear invasionlike south of their breeding range. The methods described herein will help future studies document the percentage of different age groups of Snowy Owls during such invasions and shed light on the influence of variation in prey abundance and reproductive success on the migration of this apex predator of the Arctic.

Methods

In early summer 2015 a superpeak of lemmings *Lemmus sibiricus* was registered on Beliy Island north of Yamal peninsula (73º19'N, 70º1'E; Figure 1). The abundance of lemmings was estimated by snap-trapping. Considerable numbers of Snowy Owls settled here as a result of the abundance of lemmings. On 7, 9, 13, and 15 July a total of 69.7 km was covered on foot (Figure 2, Table 1). Snowy owls were approached and photographed with a Nikon D90 with a 70-300 mm Nikon lens.

Images were sorted by number, time and date recorded on the image files. Images suitable to sex and age the owls were treated in Adobe Photoshop to enhance details of molt and bar patterns in wings (Figure 3). The birds were aged analysing moult patterns described by Solheim (2012) and later collected moult data (Solheim 2017), and individuals were recognized by bar and moult patterns in their wings (cnf. Solheim 2016).

A GPS track file was used to record the location of the owls that were photographed and subsequently aged and sexed (Figure 2). The spacing of the images helped when comparing images of birds of similar age to determine if they were the same (Figure 4) or different individuals (Figure 5).

Results

The lemming trap-index reached 13.7 animals per 100 trap-nights, which is the highest value ever measured on the Yamal peninsula since 1999 (Unpublished data). At most 89 individual Snowy Owls were seen from one vantage point. Judged by the number of owls encountered along the track routes, probably at least 150 Snowy Owls were present in the area surveyed. A total of 344 images were captured of both perching and flying birds. Of these 114 images showed flying birds and could be used for closer inspection to check the birds´ age and identity. Many of these images were however series of the same bird as it took off. The best images showing upper side of one wing and later the other wing (upstroke and downstroke from side view; Figure 6) were used to determine moult stage. It was possible to age 11 males and 14 females (Table 2). Fouteen individuals were juvenile or second calendar year birds (2CY) in their first moult (five males, nine females). six birds (two males, four females) were in later moult stages with still recognisable juvenile flight feathers in their wings (Figure 7), while only five individuals (four males, one female) were classified as adult 5CY+ birds in their fourth moult stage or later, recognised by the total lack of juvenile flight feathers in their wings.

Discussion

When encountering Snowy Owls it is recommended to take as many flight images as possible before the bird advances too far off. With modern digital photography there are no serious limitations to how many images one can secure, as in former days when expensive film set a limit to such photographying. The camera should be set to multiple image shooting at the highest speed possible for the camera at hand, and usually at ISO values of 1000-3200 to freeze the wing motion of a flying owl.

It is usually possible to use images to recognise moult stage 2 and 3 in Snowy Owls based on number of juvenile feathers left in the wings and differences in contrast and wear of molted, adult feathers (Solheim 2012, 2017), provided that the image clearly shows all secondaries and primaries (see Solheim 2016). On images of flying birds, the innermost secondaries may be hard to judge, and non-adult birds after their first moult have thus been categorized as 3-4CY, although several of the aged birds in this category seemed to be in their third moult (4CY).

Only five individuals (20%) of the aged birds were fully grown, thus hatched in 2011 or earlier, while the 14 juvenile birds made up more than half of the aged birds (56%). These birds were hatched in 2014, while the rest of the group (six individuals; 24%) were hatched in 2012 or 2013.

Since 80% of the aged Snowy Owls on Beliy in summer 2015 were hatched in the period 2012-14, the question arises where did they originate from. Snowy Owls were found nesting in Fennoscandia in 2007, 2011 and 2015. The Norwegian Snowy Owl Project equipped three male and nine female Snowy Owls with satellite transmitters in Norway in 2011 (Jacobsen et al. 2012). During summer 2012 and 2013 these owls moved along the Russian Arctic from Kola peninsula to Novaja Zemlya and Vaygach Islands, with Novaya Zemlya as the most probable area for breeding (Jacobsen et al. 2013). Adult Snowy Owls equipped with satellite transmitters in Norway documented that Snowy Owls breeding in Scandinavia in peak lemming and vole years move to Russia as far east as the Taimyr peninsula (75° N 100° E) (Solheim et al. 2008, Jacobsen et al. 2009, 2013), and even to the October Revolution Island (80° N 99° E) (Jacobsen et al. 2014) during years with no or few lemmings in Scandinavia.
According to information provided through the arctic birds conditions survey (www.arcticbirds.net), 2014 was a good breeding year for Snowy Owls in western Taymyr (Kharitonov, 2014). It is thus highly probable that the young 2-4CY Snowy Owls which made up most of the Snowy Owls on Beliy in July 2015, may have been hatched in the same part of the Russian Arctic, between Novaja Zemlya and Taimyr. Snowy Owls thus seem to make up one sub-population from Fennoscandia to Taimyr.

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Table 1 Distance in km travelled on foot during four days on tundra on Beliy Island, July 2015, number of photos of owls taken, and number of images enhanced and checked for molt and individuality.

Date	km	images	used
7 July	20.4	64	28
9 July	18.3	167	48
13 July	8.6	32	7
15 July	22.4	81	31
Total	69.7	344	114

Tabel 2 Age and sex of Snowy Owls on Beliy Island, July 2015, as judged from images. *: Bird found dead.

	Males			Females			
Date	2CY	3-4CY	5CY+	2CY	3-4C	5CY	Sum
7.7.	1			4			5
9.7.	3		2	3	1*	1	10
13.7.	1			1			2
15.7.		2	2	1	3		8
Sum	5	2	4	9	4	1	25

Figure 1 Location of Beliy Island (red circle), Russia, where Snowy Owls were seen in great numbers in July 2015.

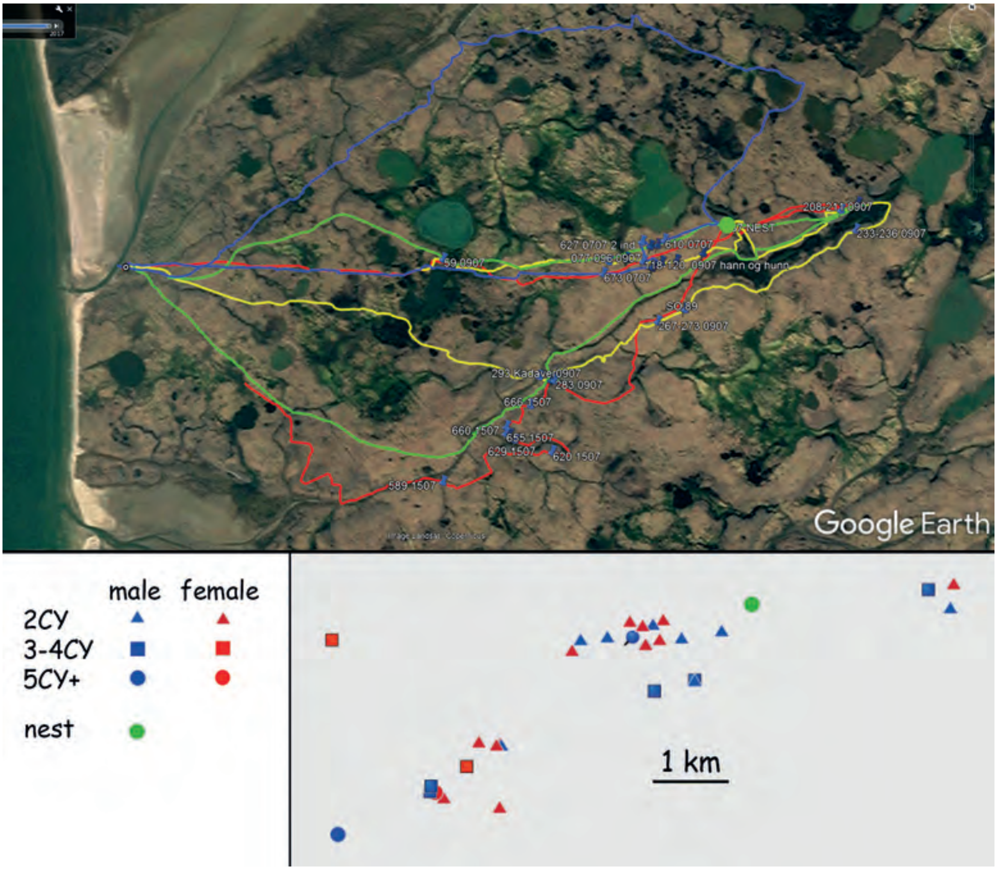

Figure 2 Walking routes (July 2015) from where Snowy Owls were encountered and photographed on Beliy Island, Russia. Blue = 7 July, Yellow = 9 July, Red = 15 July, and Green = 17 July. Key and locations of sexed and aged birds (see text) appear below the Google map.

Figure 3 Original, unedited image (left) of flying female Snowy Owl on Beliy Island, Russia, with Photoshop-edited image (right). On left wing this female has moulted P7, while on right wing both P7 and P8 have been moulted (moulted feathers not regrown). The bird is a second calendar year (2CY) individual in its first moult.

Figure 4 (Next page) Snowy Owl images 619 and 644 taken 7 July at 13:13:52 and 13:38:18 on Beliy Island, Russia. The points where the images were captured are plotted along the track route, both points linked with yellow line. The images were captured 240 m apart, and with almost 25 minutes between them. The enhanced images of the males seem to be uncannily similar judged by spots and marks on the bodies. At both instances the bird took flight shortly thereafter and were photographed flying (images 621 and 657). When comparing the dark bars on the primaries, it is obvious that these images depict the same individual. The bird must have landed further away along the track route, to be encountered again 25 minutes after first observation. This male has moulted P7 on both wings, and is a second calendar year (2CY) bird in its first moult.

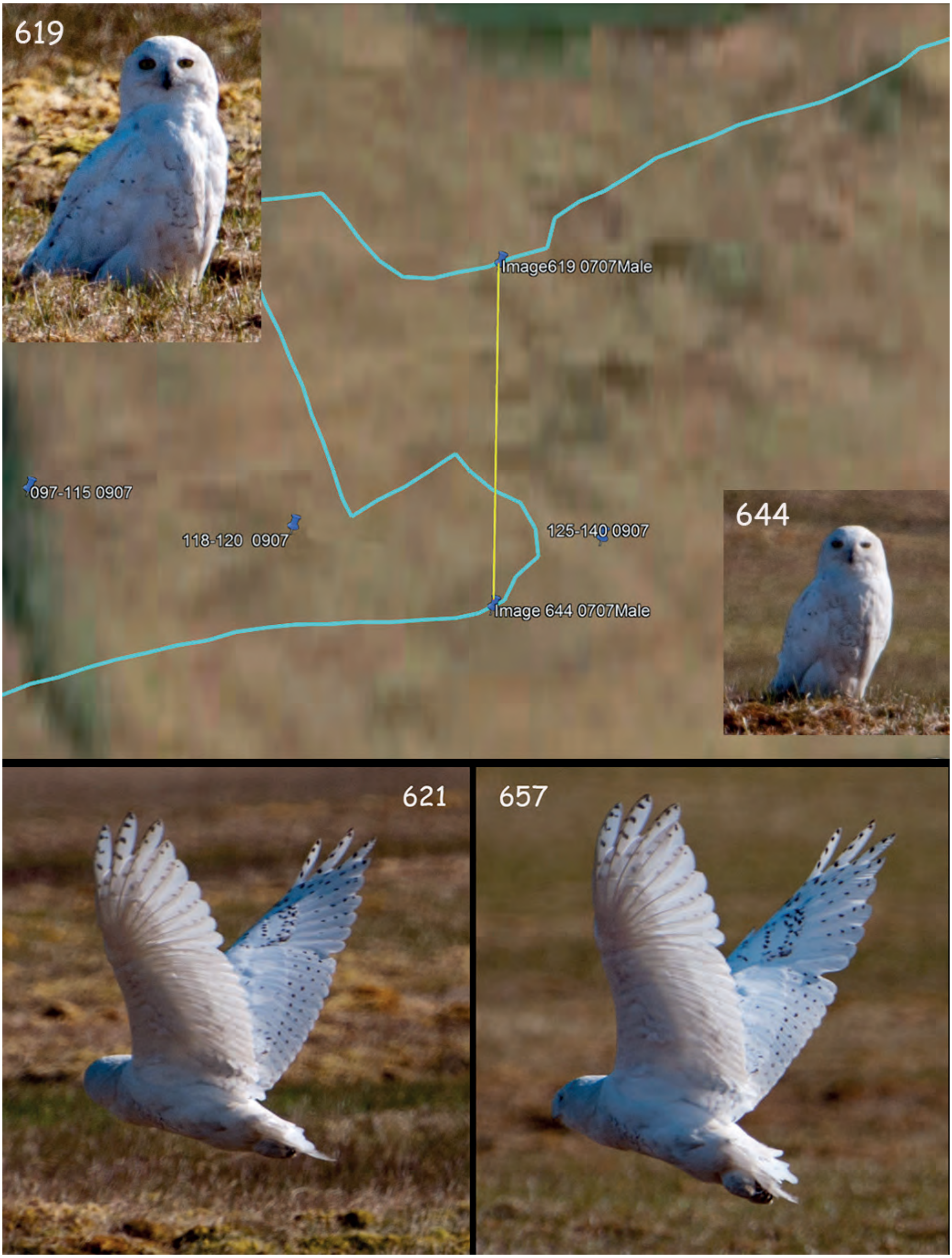
619
Image619 0707Male
097-115 0907
118-120 0907
125-140 0907
Image 644 0707Male
644
621
657

Figure 5 Snowy Owl images 666 and 673 captured 7 July at 13:41:59 and 13:51:30 on Beliy Island, Russia. Dark bar number four on inner vane from the tip of P10 and P9 is differently aligned with bars on outer vane on these two images, demonstrating that these are two different individuals. Both are second calendar year (2CY) birds in their first moult.

Figure 6 Snowy Owl images 092 and 094 captured 9 July on Beliy Island, Russia. It is a second calendar year (2CY) male taking off, showing upper side of right and left wing. The bird has moulted P7 in both wings (missing, not regrown), all other primaries are juvenile.

Figure 7 Snowy Owl image 616 captured 15 July on Beliy Island, Russia. This female has formerly moulted P7 and P8, while P9 has been moulted in 2015. P10 is still juvenile, as are three of the innermost primaries. P6 is growing, while P5 may have been moulted, or may be the outermost of the three juvenile feathers in line inwards. The bird has at least moulted once before 2015, and most possibly twice. To judge if it is third or fourth calendar year bird, all secondaries would have to be inspected, which is not possible on this image. The owl is thus classified as a third-fourth calendar year (3-4CY) bird.

PAPER V

Great Grey Owl pair nesting on an old birch snag in Ringsaker, Hedmark. June 8, 2017. Photo: Roar Solheim.

Age structure in a newly established and expanding population: high proportion of young individuals among nesting Great Grey Owls

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Abstract

The mechanisms behind expansions of bird populations and the ensuing establishment of new populations are poorly known. The distribution of the Great Grey Owl (*Strix nebulosa*) in the western Palearctic has generally expanded towards southwest during the past fifty years, and particularly so in Fennoscandia. In the past decade, the recorded breeding population in Hedmark county in south-eastern Norway, bordering Sweden, increased from 1 pair in 2009 to > 100 pairs in 2017-2018, extending the southwestern border of the distribution > 100 km. We studied the age distribution of this expanding breeding population based on the molting pattern of the wing feathers of birds captured at the nest site for banding and non-captured birds photographed in flight. The Great Grey Owl is a small mammal specialist which in the western Palearctic in particular relies on *Microtus* voles, which fluctuate in 3-4 years cycles. The proportion of 1 year old individuals among the nesting Great Grey Owls was higher in the peak phase of each small mammal cycle (2011, 2014 and 2018) than in the preceding increase phase year (2010, 2013 and 2017), and was particularly high (77%) in the first peak (2011) when the owl population was far lower (22 nest recorded) than in later peaks (64 nests in 2014 and 103 in 2018). Thus, this population seem to have been founded to a large extent by birds nesting as 1 year olds, and most likely having dispersed from Sweden where they were hatched in the previous vole increase year. The ability to determine the age of birds without having to capture them extended our data set, in particular for males, which are more reluctant to attack intruders at the nest site and therefore less likely to be captured for ringing. Being able to age a bird without having to capture it is important, because trapping does not sample a bird population randomly.

Introduction

The colonization of new areas by a bird species through natural expansion of the breeding range, from the arrival of the first individuals to the establishment of a population, is fundamental for our understanding of avian speciation and population ecology in general, and of the effects of human activities including climate change, in particular. Still, the mechanisms behind such expansions are poorly known, mainly because such events are rarely directly observed in detail. For instance, the expansion of the Western Bluebird (*Sialia mexicana*) and resulting displacement of the Mountain Bluebird (*Sialia currucoides*) in Montana, USA was caused by selection for highly aggressive dispersing males of the former species (Duckworth and Badyaev 2007). An alternative mechanism would be enhanced behavioural plasticity, or a founder´s effect.

The Great Grey Owl (*Strix nebulosa*) has a circumpolar distribution in the boreal forest of the Paleractic and Nearctic (Cramp 1985). In the western Paleartic, its range has for a long time extended through central Finland into northern Sweden (Cramp 1985). In the course of the last fifty years, however, the breeding range of the Great Grey Owl in Fennoscandia has undergone an expansion towards southwest (Stefansson 1997, Sulkava and Huhtala 1997, Valkama et al. 2011, Ottosson et al. 2012, Ławicki et al. 2013). In particular, during the last decade a remarkable colonization of c 10 000 km^2 in central parts of Hedmark county in south-eastern Norway on the border to Sweden has occurred (Berg 2016, Berg et al. 2019), extending the breeding range >100 km towards southwest (Fig. 1). Here, the number of recorded breeding pairs has increased from one in 2009 and three in 2010 to > 100 in 2017 and 2018 (Fig. 2a), probably being representative of the expansion of a greater real breeding population (Berg 2016, Berg et al. 2019). In 2017 and 2018, another two nests were found even further to the south and west in two other counties (Haga and Bjerke 2017, Steen and Midtgard 2019). This expansion has been possible to follow in detail because Great Grey Owls have an iconic appearance, are large (male body mass c. 900 g) and not very shy, and are often active at daytime foraging by perching in open habitats (Cramp 1985). Hence, they may quite easily be spotted by ornithologists and members of the public. In addition, the fact that Great Grey Owls nest in abandoned stick nests made by large raptors, in particular Northern Goshawk (*Accipiter gentilis*) and Common Buzzard (*Buteo buteo*), which had been monitored by local ornithologists for many years before the first Great Grey Owl was found (Berg et al. 2011), has facilitated the recording of breeding pairs. Putting up man-made nesting platforms as raptor nest surrogates has added to this ability to monitor the expansion of the Great Grey Owl population. In fact, the proportion of the recorded Great Grey Owl nests in Hedmark county located at such platforms has increased from 12% in 2010-2013 to 48% in 2016-2018 (Berg et al. 2019). Ornithologists have been eager to capture and ring the breeding owls, and to take photos of them, and this has given the opportunity to estimate their age.

In long-lived owls and birds of prey most individuals do not start breeding as early as they are physiologically able to, and commonly delay breeding until they are at least 2-3 years old. The optimal age at first breeding is affected by a complex interplay between costs and benefits of early breeding mediated by habitat heterogeneity and population density (Krüger 2005). Apart from the fact that some individuals have been recorded breeding as 1 year old (Cramp and Simmons 1980, Cramp 1985), data on age of first time breeders are limited for most species. In the Tawny Owl (*Strix aluco*), 70% started to breed as 1 year old in a population in southern Finland, with no difference between the sexes (Karell et al. 2009), while in a population in northern UK, only 27% of males and 14% of females started breeding as 1 year olds (Millon et al. 2010). In the larger Ural Owl (*Strix uralensis*), 16% started to breed as 1 year olds in a population in southern Finland (Brommer et al. 1998). In a population of the Northern Goshawk in Germany, 42% started to breed as 1 year olds (Krüger 2005).

Breeding owls have traditionally been aged based on being banded as nestlings and later controlled as nesting adults (cf. Stefansson 1997). Molt patterns in the wings of owls can however be used to age the birds as long as some juvenile flight feathers are still present (e.g. Pietiäinen and Kolunen

1986, Hörnfeldt et al. 1988, Suopajärvi and Suopajärvi 1994, Solheim 2011a, b, 2012). Photos of a flying owl where the wings are fully stretched may reveal the age of the bird without having to capture it. This makes it possible to age more individuals than the ones which can be captured and examined in hand, and can even be used to recognise or separate different individuals (Solheim 2010, 2016). Being able to age an owl without having to capture it is important, because the probability of trapping an individual bird depends on its personality, implying that trapping does not sample a population randomly (Garamszegi et al. 2009).

Great Grey Owls in Fennoscandia subsist almost exclusively on shrews and microtine rodents, and in particular on *Microtus* voles (Mikkola 1983, Cramp 1985). Therefore, they show a strong numerical response to the 3-4 year microtine rodent cycle, and rarely nest in years other than the pre-peak increase year and the peak year, i. e. in two of the 3-4 years in each cycle (Hipkiss et al. 2008). Here, we show that the proportion of 1 year old individuals among breeding individuals in a newly established and expanding population of Great Grey Owls in Norway was higher in the microtine rodent peak years than in the increase years, and exceptionally high in the first peak year after the establishment of the population.

Materials and methods

The 344 nestings of Great Grey Owls recorded in Hedmark county during 2009-2019 were located in 14 municipalities in the southern half of the county (for details, see Berg et al. 2019). These 14 municipalities cover a total land area of 14 777 km^2 (Fig. 1). The central parts of this area, where the majority of the nesting were recorded (see Berg et al. 2019), cover c 3 000 km^2 (Fig. 1). The number of recorded nestings in each municipality (1-59) was not significantly correlated with the land area of the actual municipality (Spearman´s rank correlation, $r_s = 0.12$, $p = 0.69$).

As many as possible of the recorded breeding owls and their chicks were captured for banding or control of formerly banded individuals. Chicks were banded either as grown nestlings or shortly after they had left the nests, before they were able to fly properly. Adult Great Grey Owls often defend their nest and grown chicks by approaching and fiercely attacking humans who come too close (Stefansson 1997). Attacking owls were captured in large scoop-nets, a doughasa net or with a noose-line on a telescopic fishing rod when an owl was perching close by without attacking. A total of 155 adults (30 males and 135 females) and 543 chicks were banded, and 48 adult breeders, of which three had been banded as nestlings in Sweden, were controlled a total of 71 times (Table 1). Individuals that could not be captured were photographed if possible. A total of 278 nesting adult owls (64 males and 214 females) were aged, which is 40.4% of the 688 assumed individuals in the recorded 344 nestings during 2009-2018 (Table 1).

The ageing categories for birds proposed by Runde (1991) were used. A bird is in its first calendar year (1CY) from the time of hatching until 31 December. In the following year it is 2CY, and so on. A bird is denoted 5CY+ when it is in its fifth calendar year or older. The birds were aged using the molt schemes described by Suopajärvi and Suopajärvi (1994) and Solheim (2011a), supplied with later experiences with birds in age category 5CY. For some owls photos of the bird´s tail only and not the wings were obtained, so it could only be decided whether the owl had molted its juvenile retrices or not. These individuals were thus classified as either juveniles (2CY) or older adults (3CY+).

We used one individual owl in one nesting attempt as population unit in statistical tests. The 64 nesting males and 214 nesting females that we scored for age were from 217 different nests. Of these 278 owls, 225 were captured for ringing or control, and then aged when handled, while 53 (19.1%) were photographed without being captured, and aged from the photo only (Table 1). Excluding repeated captures of the same individuals in different years to avoid pseudoreplication, we were left with 62 different males and 161 different females scored for age. Individuals being photographed, but not captured, in one year may have been captured or photographed in a later year and still recorded as different individuals. Such cases are few or none.

As in index of the abundance of prey for the great grey owls during the breeding season in 2009-2019 we used data collected in spring from a long-term trapping study on fluctuations of the small mammal populations in the northern boreal forest, conducted within our study area (Fig. 1). The distance from this site to the nearest recorded great grey owl nesting is c 10 km, the distance to the core great grey owl breeding area is 30-40 km, and the distance to the recorded nest furthest away is c. 130 km. The site and the trapping method are described by Sonerud (1986, 1988) and Selås et al. (2013). For the purpose of this study, we use the trapping index of all small mammals species pooled, i. e. *Microtus* voles (Field vole *M. agrestis* and Tundra Vole *M. oeconomus* pooled), bank vole (*Myodes glareolus*), Wood Lemming (*Myopus schisticolor*) and shrews (Soricidae; almost only common shrew (*Sorex araneus*)), because these are all delivered at great grey owl nests (Mikkola 1983, Cramp 1985). In addition, we refer to a corresponding trapping index based on data collected in fall by Wegge and Rolstad (2018) at a site in the southern part of Hedmark county c 110 km south of the other trapping site (Fig. 1). All recorded great grey owl nestings were located < 100 km from one of these trapping sites, and most < 50 km from the northern site (Fig. 1). Together, the small mammal population fluctuations recorded at these to sites would fairly well reflect the situation in our study area, as the small mammal populations at these two sites fluctuated in close synchrony.

Data analysis

For each case of an owl observed nesting, we measured the following explanatory variables: 1) Age of the individual (Table 2). 2) Sex of the individual. 3) Study year, taken as a categorical variable. Because there were few observations in 2009 and 2010, these two years were pooled in the analysis. 4) Whether the individual had been captured for ringing, and its age determined when having the bird in the hand, or whether the individual had been photograped only, and its age determined later from the photo (Table 1).

The proportion of females among the owls observed was not significantly related to study year, neither when all observations were included (X^2 = 8.81, df = 5, p = 0.12), nor when only the first observation of each individual observed breeding in two or more years was included (X^2 = 6.38, df = 5, p = 0.27). The proportion of individuals that had only been photographed among was not significantly related to study year, neither when all observations were included (X^2 = 8.57, df = 5, p = 0.13), nor when only the first observation of each individual observed breeding in two or more years was included (X^2 = 4.93, df = 5, p = 0.42). The sex of an owl observed nesting was, however, highly correlated with whether the owl had been photograped only, both when all observations were included (9.8% of females vs. 50.0% of males; X^2 = 51.56, df = 1, $p < 0.0001$) and when only the first observation of each individual observed breeding in two or more years was included (12.4% of females vs. 51.6% of males; X^2 = 38.45, df = 1, $p < 0.0001$). This is due to the fact that males are far more difficult to capture than are females, because they show less aggression towards intruders at the nest and are thus less likely to attack or approach close enough to allow a capture attempt.

For the statistical analysis each nesting owl was classified as either young (2 CY) or old (3 CY+), and the effects of year, sex, and method of age classification were analyzed by using logistic regression in JMP® Pro version 13.0.0 (SAS 2019). We created models with different combinations of the explanatory variables and their first-order interactions. To be cognitively tractable no model included more than one interaction. Candidate models were ranked using the Akaike information criterion corrected for small sample size (AICc), following recommendations by Burnham et al. (2011) and Richards et al. (2011). For each analysis, the ten lowest-ranked models, and the model with only intercept, are presented (Supplementary file). Models with DAICc < 2.0 were considered to be well supported and thus competing with the model with lowest AICc value. Among competing models, the one with the lowest number of effects was considered the most parsimonious. For each variable we also calculated AICc weight. For the most parsimonious models we provide post-hoc tests. Estimates are given with ± 1 SE.

Results

The small mammal populations in our study area during the Great Grey Owl breeding season, as measured in May annually near the core area (Fig. 1), fluctuated markedly with low levels in 2009, 2009, 2015 and 2019, with increase year in 2010, 2013 and 2016-2017, and with peak year, i. e. the last year before the crash year, in 2011, 2014 and 2018 (Fig. 2a). This pattern was closely followed by the number of recorded Great Grey Owl nestings when corrected for the long-term increase in population size (Fig. 2b).

Of the nesting owls observed, 11.9% were scored as young (2CY) when all observations were included (9.8% of females and 18.8% of males; $X^2 = 3.76$, df = 1, p = 0.053), and 14.8% when only the first observation of each individual observed breeding in two or more years was included (13.0% of females and 19.4% of males; $X^2 = 1.41$, df = 1, p = 0.23).

The best model to explain the proportion of young individuals (2 CY) among the owls observed nesting included year only, both when all observations were included (Table S1) and when only the first observation of each individual observed breeding in two or more years was included (Table S2). Adding the sex of the owl to the model, or adding the method of aging, i.e. whether the owl had been captured or only been photographed, in various combinations did not improve the model fit (Tables S1 and S2). The evidence ratio of the best model to the second best model was 2.6 in both cases (Tables S1 and S2). Hence, the further analysis focuses on the effect of year only.

The proportion of young owls was significantly higher in 2011 (76.9 %) than in any other study year, both when all observations were included (Fig. 3, Table 3), and when only the first observation of individuals observed breeding in two or more years was included (Table 4). In addition, the proportion of young owls was significantly higher in 2018 (15.4%) than in 2017 (1.8 %) and 2013 (0 %) when only the first observation of individuals observed breeding in two or more years was included (Table 4), and significantly higher in 2018

(9.9%) than in 2017 (1.5 %) and marginally non-significantly higher in 2018 than 2013 (0 %) when all observations were included (Table 3).

To sum up, during our study the proportion of 1 year old individuals among the breeding Great Grey Owls was higher in each of the three years preceding the crash in the small mammal populations (2011, 2014 and 2018) than in the preceding small mammal increase year (2010, 2013 and 2017), significantly so in 2010-2011 and 2017-2018, but not in 2013-2014 (Fig. 3, Table 3).

Discussion

Among the breeding Great Grey Owls in our study, 12% were 1 year old, and 16% were 1 or 2 years old. In the first peak year 2011, 77% were scored as 1 year old, compared to 5% in the other years. Including the 2 years old owls, the corresponding figures were 77% and 9%, respectively. Thus, in the years other than 2011, 91% of the breeding owls were at least 3 years old. In an established population of the Great Grey Owl in northern Sweden, only 4% of the nesting individuals were scored as 1 year old, and another 5% as 2 years old, thus 91% of the individuals were scored as 3 years or older (Solheim and Stefansson 2016). Thus, the age distribution of our study population from 2013 onwards was remarkably similar to that in the established population in northern Sweden. The aging of nesting owls in the Swedish population was, however, based on controls of birds banded as chicks only, and not on wing feather characteristics (cf. Solheim 2011a).

The year with the exceptional high proportion of 1 year old individuals among the breeding Great Grey Owls in our study was preceded by the small mammal increase year 2010 and followed by the low year 2012 (cf. Wegge and Rolstad 2016). Thus, the 1 year old owls were hatched in the pre-peak year 2010. The proportion of 1 year olds among the nesting Great Grey Owls was relatively high in 2014 (7%) and 2018 (13%), which both were years preceded by an increase year (2013 and 2017, respectively) and followed by a low year (2015 and 2019, respectively; cf. Wegge and Rolstad 2016). In a population of Ural Owls in Finland, 16% of the nesting individuals were 1 year old (Brommer et al. 1998). Here, nesting as a 1 year old was conditional on being hatched in the pre-peak vole year; 42% of the breeding Ural Owls were 1 year old in the vole peak year, compared to only 3% in the pre-peak year and 0% in the low year (Brommer et al. 1998). In a population of Tawny Owls in northern England, where the population density of its main prey species, the Field Vole (*Microtus agrestis*), fluctuated with a 3 year cycle, owls of both sexes that started to breed as 1 year old birds did so almost exclusively in the years with peak vole density in spring, whereas those that were 2 years or older when breeding for the first time did so in low or increase vole years (Millon et al. 2010). Similarly, in a population of Tawny Owls in southern Finland where voles also exhibited a 3 year density cycle, age at first breeding was lowest for owls starting to breed in the year with peak vole density in spring, and higher for those starting to breed in the low or the increase year of the vole cycle (Karell et al. 2009).

The proportion of 1 year old Great Grey Owls in our study was much higher in 2011 than in the corresponding peak phase of the two next vole cycles (2014 and 2018). The population density of Great Grey Owls in our study area was far lower in 2011 (22 nestings recorded) than in 2014 (64 nestings recorded) and in 2018 (103 nestings recorded). Thus, the proportion of 1 year old owls nesting declined as the population density increased. Similarly, in a newly established population of the Northern Goshawk in Hamburg, Germany, a large proportion of breeding recruits were 1 or 2 years old (Rutz 2008). This is characteristic of young or expanding Northern Goshawk populations, while in undisturbed, established populations, first-time breeders are usually at least 3 years old (Rutz et al. 2006). In both sexes of the Eurasian Sparrowhawk (*Accipiter nisus*) in the UK the proportion of 1 year old breeders was higher in a newly established and expanding population than in an established and stable population and a declining population (Wyllie and Newton 1991).

The proportion of 1 year old Great Grey Owls tended to be higher among nesting males than among nesting females. Similarly, age at first breeding was lower among males (median 2 years) than among females (median 3 years) in a population of Tawny Owls in northern England (Millon et al. 2010). However, it was not so in a population of Tawny Owls in southern Finland (Karell et al. 2009).

The high proportion of 1 year old Great Grey Owls breeding in our study area in 2011 was probably due to natal dispersal of birds hatched further east in Sweden in 2010. This is also the most likely explanation for the steep rise in number of nests and nesting attempts in our study area from 2010 to 2011 (from 3 to 22). Raptor nests were monitored by local ornithologists for many years before 2010 in Elverum municipality in Hedmark in the core of our study area (Berg et al. 2011). The 22 nesting pairs found in 2011 were thus not formerly undisclosed breeding owls, and must have newly arrived in the area. The fact that one of the breeding Great Grey Owls that were controlled breeding in our study area in 2011 had been banded as a nestling in 2010 in Dalarna county in Sweden, 126 km to the east, supports this interpretation. Also a female controlled breeding in our study area in 2017 was banded as a nestling in Sweden in 2010, 325 km towards northeast, supporting our view of 2010 as a year of good reproduction for Great Grey Owls in mid-central Sweden. A third Swedish-banded female was controlled breeding in our study area in 2010, 159 km west of where she had been banded as a nestling in 1999. As a curiosity, she was hatched only 440 m from the nest where the female controlled in 2011 was hatched, although 11 years earlier. In an established population of the Great Grey Owl in northern Sweden, mean natal dispersal distance was 40 km for females breeding as 1 year olds and 76 km for all females (Solheim and Stefansson 2016).

We do not know much of what the Great Grey Owls hatched in our study area in the small mammal increase years 2013 and 2017 were doing in the small mammal peak years 2014 and 2018, respectively, apart from the fact that two females banded as nestlings in 2013 were controlled nesting 2 km and 25 km away, respectively in 2014, and that a third female banded as nestling in 2017 was controlled nesting 15 km away in 2018. Most of the owls hatched in our study area in 2013 and 2017 were certainly not among the nesters recorded and aged here in 2014 and 2018. These 1 year old birds may therefore either have postponed nesting, or dispersed into other parts of south-eastern Norway in a still expanding population. Of the 66 aged breeders in 2014 no less than 25 (39%) were 4CY and 5CY birds , which indicates that 2010 and 2011 were really good production years for Great Grey Owls in south-central Scandinavia. This was also reflected in the age distribution of the non-breeding Great Grey Owls observed in Norway and Sweden in 2012, with a high proportion of 2CY birds (Solheim 2014b).

In conclusion, the Great Grey Owl population of >100 recorded nesting pairs in south-eastern Norway in 2017-2018 seem to have been founded to a large extent by birds nesting as 1 year olds in 2011, after most likely having dispersed towards southwest from Sweden. Our data set on the age of the nesting owls was extended due to the possibility to determine the age of the birds from photos without having to capture them. This was particularly valuable in the case of males, which are more reluctant than females to approach and attack intruders at the nest site and therefore less likely to be captured for ringing. Being able to age an owl without having to capture it is important, because trapping does not sample a bird population randomly (Garamszegi et al. 2009). Future studies on age structure in owl populations should sample data by taking pictures of the owls in flight in addition to, or instead of, capturing them.

Author contributions RS originally formulated the idea, RS and TB developed the methodology and collected the data on the owls, GAS collected the data on the small mammals, RS, TB and GAS organized the data, GAS did the statistical analysis, GAS and RS wrote the paper, and TB made editorial contribution.

Data availability Data sets analyzed during the study can be made available on reasonable request.

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Conflicts of interests The authors declare that they have no conflict of interest in the authorship of this article. Use of product or corporation names is for descriptive purposes only and implies no endorsement by any author or affiliation.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Table 1 Number of breeding Great Grey Owls aged after having been captured and banded or controlled, or only been photographed in flight without being captured, during 2009-2019 in Hedmark county, Norway

Year	Number of aged individuals				Number of nestings recorded
	Banded	Controlled	Photo	Total	
2009	0	0	2	2	1
2010	4	0	0	4	3
2011	15	3	8	26	22
2012	0	0	0	0	0
2013	21	4	5	30	30
2014	36	13	17	66	64
2015	0	0	0	0	0
2016	0	0	0	0	2
2017	40	17	12	69	119
2018	38	34	9	81	103
2019	0	0	0	0	0
Total	154	71	53	278	344

Table 2 Number of breeding Great Grey Owls aged during 2009-2019 in Hedmark county, Norway, separated on age class (calendar year, CY), where 3CY+ denotes individuals in their third calendar year or older, 4CY+ denotes individuals in their fourth calendar year or older, and 5CY+ denotes individuals in their fifth calendar year or older.

Year	2 CY	3 CY	3 CY+	4 CY	4 CY+	5 CY	5CY+	Total
2009	0	0	0	0	0	0	2	2
2010	0	1	0	0	0	0	3	4
2011	20	0	0	0	0	0	6	26
2012	0	0	0	0	0	0	0	0
2013	0	6	0	8	0	0	16	30
2014	4	0	6	19	0	4	33	66
2015	0	0	0	0	0	0	0	0
2016	0	0	0	0	0	0	0	0
2017	1	1	1	6	1	2	57	69
2018	8	2	0	0	0	6	65	81
2019	0	0	0	0	0	0	0	0
Total	33	10	7	33	1	12	182	278

Table 3 Test of differences between the study years in the proportion of 1 year old individuals among breeding Great Grey Owls, when a) all cases recorded are included, and b) only one case of each individual owl recorded is included. For each combination of two years, the upper value is Pearson chi-square, and the lower value is p. Significant values are in bold, and marginally non-significant values are in italic .

Year	2011	2013	2014	2017	2018
a)					
2010	**12.31**	0.00	0.39	0.09	0.65
	0.0005	1.00	0.53	0.77	0.42
2011	-	**35.90**	**48.58**	**62.47**	**45.79**
	-	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
2013	-	-	1.90	0.44	*3.19*
			0.17	0.51	*0.074*
2014	-	-	-	2.01	0.71
				0.16	0.40
2017					**4.69**
					0.03
b)					
2010	**12.31**	0.00	0.46	0.11	1.07
	0.0005	1.00	0.50	0.74	0.30
2011	-	**32.50**	**41.76**	**53.38**	**28.53**
	-	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
2013	-	-	1.95	0.46	**4.46**
			0.16	0.50	**0.03**
2014	-	-	-	1.94	1.85
				0.16	0.17
2017					**6.67**
					0.01

Fig. 1 The study area (hatched) and the core area (cross-hatched) in the southern part of Hedmark county, Norway, where a Great Grey Owl population was established in 2009-2011, with the pre-2009 distribution of Great Grey Owls in Sweden and Finland indicated. The two sites where data on small mammal population fluctuations were collected are marked with a dot. Data from the northern site are presented in Fig. 2a, and data from the southern site are presented in Wegge and Rolstad (2018).

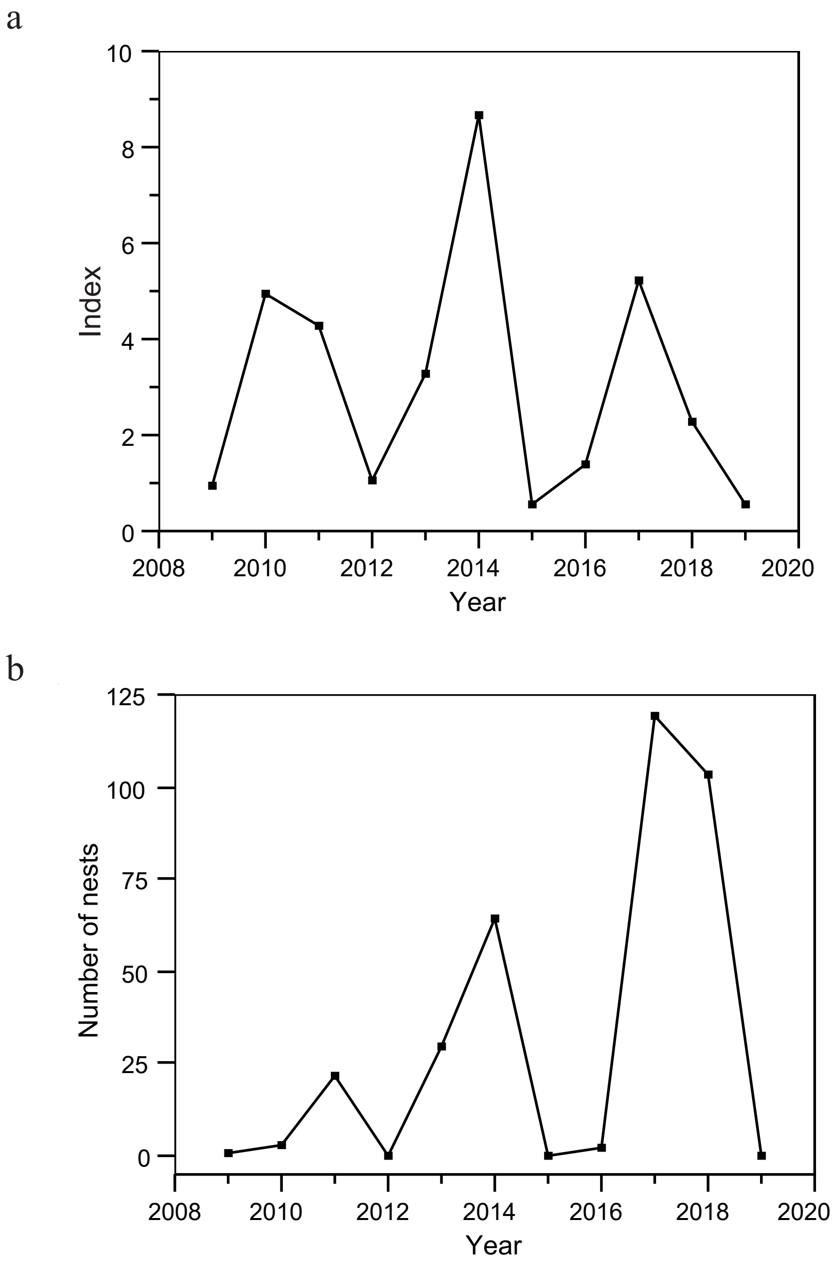

Fig. 2 Annual variation during 2009-2019 in a) spring trapping index of small mammals at the northern site in Fig. 1, and b) number of Great Grey Owl nestings recorded in Hedmark county, Norway.

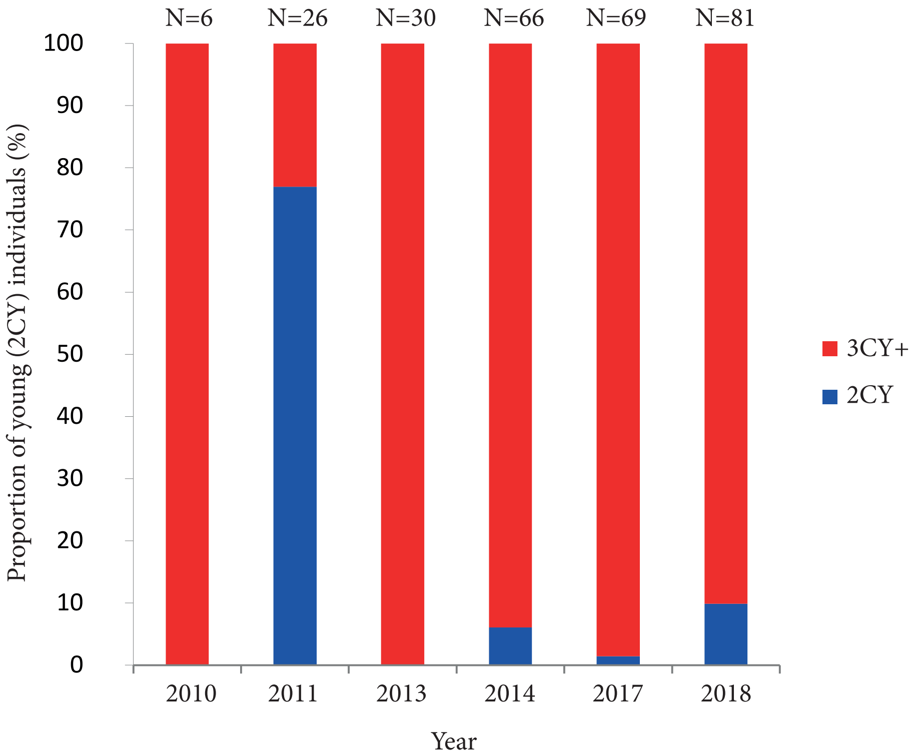

Fig. 3 Proportion of 1 year old (2CY) individuals among breeding Great Grey Owls in Hedmark county, Norway, in small mammal increase years (2009/2010, 2013, 2017) and small mammal peak years (2011, 2014 and 2018). Data from 2009 and 2010 are pooled and termed 2010 due to low sample size in 2009. Sample size above columns.

Table S1. Model selection to determine which variables influenced whether a breeding great grey owl (*Strix nebulosa*) was 1 year old (2CY) or older (3CY+), when all observations were used (n=278). Models with ΔAIC ≤ 2.0 from the best model are shown in bold. Only the ten best models, and the model with intercept only, are shown. AIC weight (w) is shown for the ten best models.

Variables	LogLikelihood	df	AICc	ΔAIC	AIC w
Year	**-40.81**	**5**	**133.26**	**0.00**	**0.500**
Year Sex	**-40.91**	**6**	**135.16**	**1.90**	**0.194**
Year Method	-40.82	6	135.34	2.08	0.177
Year Sex Method	-40.98	7	137.15	3.89	0.072
Year Sex Method Sex*Method	-41.77	8	137.71	4.45	0.054
Year Sex Year*Sex	-41.75	11	144.25	10.99	0.002
Year Method Year*Method	-41.03	11	145.70	12.44	0.001
Year Sex Method Year*Sex	-41.88	12	146.19	12.93	0.001
Year Sex Method Year*Method	-41.18	12	147.60	14.34	<0.001
Sex	-1.72	1	203.18	69.92	<0.001
Intercept	<0.01	0	204.59	71.33	

Table S2. Model selection to determine which variables influenced whether a breeding great grey owl (*Strix nebulosa*) was 1 year old (2CY) or older (3CY+), when only the first case of each individual great grey owl recorded breeding twice or more is included (n=223). Models with ΔAIC ≤ 2.0 from the best model are shown in bold. Only the ten best models, and the model with intercept only, are shown. AIC weight (w) is shown for the ten best models.

Variables	LogLikelihood	df	AICc	ΔAIC	AIC w
Year	**-37.67**	**5**	**124.02**	**0.00**	**0.512**
Year Method	**-37.78**	**6**	**125.91**	**1.89**	**0.199**
Year Sex	-37.67	6	126.13	2.11	0.178
Year Sex Method	-37.79	7	128.06	4.04	0.068
Year Sex Method Sex*Method	-38.26	8	129.28	5.26	0.037
Year Sex Year*Sex	-39.01	11	134.42	10.40	0.003
Year Sex Method Year*Sex	-39.23	12	136.23	12.21	0.001
Year Method Year*Method	-37.98	11	136.49	12.47	0.001
Year Sex Method Year*Method	-37.98	12	138.74	14.72	<0.001
Sex	-0.68	1	189.66	65.62	<0.001
Intercept	<0.01	0	188.98	64.96	

PAPER VI

Juvenile 2CY Great Grey Owl east of Arendal, Agder, April 21, 2019. On September 7, a Great Grey Owl was photographed on the same locality, showing one wing feather moult. Bar patterns in the wing of these images confirmed that it was the same individual as portrayed above. Photo: Roar Solheim.

ORNIS SVECICA 24:3–11, 2014

Age of Great Grey Owls *Strix nebulosa* observed in Scandinavia in 2012 as revealed by digital photos in the national species report archives

Ålderssammansättning hos lappugglor Strix nebulosa *observerade i Skandinavien 2012 bestämd med hjälp av digitala fotografier inskickade till Artdatabankens artportal*

ROAR SOLHEIM

Abstract

Record breaking numbers of breeding Great Grey Owls *Strix nebulosa* were reported in Sweden and Norway in 2010 and 2011, followed by 4105 observations in 2012 as revealed by the national Species archives. Based on locality id numbers, at least 144 individuals were reported with photos which could be used to age the individuals. The majority (76%) of these birds were young birds hatched in 2011 (83% including birds aged probably 2CY). Among dead owls brought to the Natural History Museum in Stockholm, the percentages of owls hatched in 2011 were similar (78% and 88%). The high percentage of young owls could be caused by young birds hunting closer to human settlement than older birds, but more likely it was caused by a higher total production of young in south-central Scandinavia in 2011 than in 2010. This study shows that photos in the national species archives reveal the age structure of the Great Grey Owl population, fundamental data to understand the current distributional expansion of this species. This method may also be applied to other species.

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Introduction

The Great Grey Owl *Strix nebulosa* has expanded its range in NW Europe the last decades (Lawicki et al. 2013). In Sweden, there was a marked increase in population size from 1960 to the late 1980s (Stefansson 1997). According to Stefansson (1997), the autumn population in Sweden was probably at least 3000 individuals in 1987, which was a very good breeding year. Since 1989 the Great Grey Owl has become a regular breeder in SE Norway (Solheim 2009a), and in 2011 a total of 22 nests or breeding attempts were recorded in the county of Hedmark (Berg et al. 2011). Also in Sweden 2011 was a record-breaking breeding year for Great Grey Owls, with an estimated late summer population of 4000–4500 individuals (Stefansson 2013). Several individuals found dead or photographed in SW Norway and Sweden in the autumn of 2009 were adult birds as judged by their moult patterns (Solheim 2009). This sparked a study of the moult sequences and patterns of Great Grey Owls, based on skinned birds ringed as nestlings (Solheim 2011). As juvenile and adult flight feathers are usually markedly different and easily recognizable, it is possible to age a Great Grey Owl at least up to the spring after its second flight feather moult. The moult patterns can also be detected on live birds in the field, and documented on digital photographs (Solheim 2009a, 2010, 2011, 2013).

Methods

The Swedish and Norwegian species report archives collect data on animals and plants (Artdatabanken.se and Artsdatabanken.no). Both countries use the same digital database based on the Swedish Species Project started in 2002, where informers can make daily entries of their observations. The bird pages are extensively used by ornithologists, both amateurs and professionals, and represent an easily accessible up-to-date register of a species´ observed distribution and recent presence in the two Scandinavian countries. When reporters document their observations with digital photos, extra information can be gained. The number of reports of Great Grey Owl observations peaked in 2012, with more than 4000 single reports filed.

I first downloaded all Swedish entries of Great Grey Owl observations up to 16 November 2012, and the remaining reports on 7 January 2013, and manually counted the number of entries by month. On 21 August 2013 I downloaded all reports on Great Grey Owl observations from Norway and on 22 August from Sweden. In the last check of the data from Sweden I sorted observations by landscape before downloading the reports. While the freely accessible number of reports from Norway for the whole 2012 was only 58, there were a total of 3998 reports from Sweden. After I gained access to the total material from Norway and Sweden, including reports with restrictions on publication, the total number of reports from Norway amounted to 107, compared to 4263 from Sweden (265 restricted reports). The Norwegian reports thus made up a mere 2.4% of all Great Grey Owl reports from Scandinavia in 2012 (Table 1). All entries with photos of the owl(s) reported were inspected on a high quality PC screen, and all images which

Table 1. Reports of Great Grey Owl observations from Sweden and Norway in 2012. For Sweden only openly accessible reports are included, which could be separated to landscape. Number of localities based on number of separable dots on the species maps as shown on the Species Archives websites. +images: images which can be used for age determination of bird. Minimum number of individuals as shown on +images. Parentheses: restricted localities included.

Rapporter om observerade lappugglor i Norge och Sverige 2012. Från Sverige är skyddade observationer ej medtagna. Antal lokaliteter är antal prickar som framkommer i varje landskapskarta från Artdatabankens register. +images: foton som kan användas för att åldersbestämma fågeln. Minimum antal fåglar på +foton. Parentes: antal med skyddade lokaler inräknade.

Landscape/ land		Min. no. of localities	Number of reports	Reports with images	Reports with +images	Min. no. of individuals
Lappland						
	T	1	1	0	0	0
	Lu	3	4	0	0	0
	Pi	10	11	0	0	0
	Ly	7	7	0	0	0
	Ås	1	1	0	0	0
Jmtl		8	12	3	2	2
Hjd		1	1	0	0	0
Nb		24	38	4	0	0
Vb		52 (53)	100	7	3	3
Ång		58	230	51	20	13
Mpd		72	299	90	55	23
Hsl		79 (81)	189	9	2	2
Dlr		37 (43)	118	27	15	5
Gstr		32	186	33	15	5
Upl		77 (81)	1059	170	40	12
Srm		70	780	166	73	31
Vstm		26 (38)	54	14	5	3
Nrk		15	106	9	5	3
Vrm		37 (39)	163	40	20	8
Ög		15	132	16	6	3
Vg		39	181	32	10	5
Dls		7	8	2	2	2
Boh		6	30	11	8	1
SM		18 (21)	130	42	18	7
HL		3	5	1	0	0
Bl		6	47	11	2	1
Sk		6	106	29	9	2
Sums						
Sweden		710 (740)	3998	767	310	131
Norway		33	107	46	13	13
Total		743 (773)	4105	813	323	144

Figure 1. Tail of young Great Grey Owl in age category 1CY–2CYs (left), showing typical juvenile feathers, compared to a tail of a bird that has moulted once (2CYa; right). The juvenile feathers are sharply pointed with a diffuse, dark crossbar close to the whitish edge. The adult tailfeathers are broader with rounded tips, and no diffuse crossbars between the outer distinctive dark crossbar and the tip of the tailfeathers. See also Figure 2 and 3. Specimens photographed in the Natural History Museum, Stockholm.

Stjärt av ung lappuggla (vänster) med juvenila fjädrar, sammanliknat med stjärt från en uggla som har ruggat första gången. Juvenila fjädrar är spetsiga med en ljus yttre kant. Adulta stjärtpennor är bredare, avrundade och utan diffusa mörka band utanför det markanta yttre tvärbandet. Se även Figur 2 och 3.

might reveal the age of the owl were downloaded for closer inspection.

Birds are aged according to the calendar year approach. A juvenile is thus 1CY until 31 December, when it becomes a 2CY bird. Because wing feather moult takes place during summer, I specified if an owl was from spring (s) or autumn (a). A 2CYs owl has not moulted any wing or tail feathers yet, while a 2CYa owl has an adult tail and some typical adult feathers in the wing. For further explanation: see Solheim (2010).

The age of most of the owls was judged by the character of their tail feathers (Figure 1). On the images where an outspread wing was in focus and visible, the moult sequence was used to age the owl after the 2Y stage. It turned out to be next to impossible to sort out localities of photos accompanying the selection of restricted reports from Sweden, so these photos were excluded in the Swedish material in Table 3.

When searching for reports in the species archives, one can choose different ways of selections and presentations. Species observations can be searched for specific periods, regions, and combinations. When presenting the reports, one can choose distribution maps, lists, histograms and others. The different ways of searching and presenting result in different numbers of reports displayed. I do not know the reason for these discrepancies, and have also been unable to find an explanation for them. However, as the listed observations are the main source for this work, I have used the numbers from these listings as the number of reports from each country and landscape (Sweden).

The downloading of Great Grey Owl reports from Sweden in January and August 2013 gave different numbers of entries. The report strings from January were manually counted for each day and month (Table 2), resulting in 3103 reports, of which 547 were supported by photos. The count from August, sorted by landscapes, gave a total of 3998 entries (Table 1), while a count of all pin-

Table 2. Great Grey Owl reports by month from Sweden 2012, as revealed by downloads from the national Species Archive on 16 November 2012 and 7 January 2013. Based on openly accessible reports only. * days with reports/days in month.
*Antal rapporter om lappuggleobservationer i Sverige 2012 när rapporterna laddades ner från Artportalen den 16 november 2012 och 7 januari 2013. Inga skyddade lokaler inräknade. *: dagar med observationer/ dagar per månad.*

Month	Days with reports*	Number of reports	Reports with images	Mean to reports per report day
January	26/31	191	46	7.3
February	29/29	188	53	6.5
March	31/31	810	142	26.1
April	30/30	616	92	20.5
May	31/31	504	67	16.3
June	30/30	207	50	6.9
July	28/31	101	17	3.6
August	27/31	69	7	2.6
September	28/30	114	26	4.1
Oktober	29/31	110	15	3.8
November	27/30	134	21	5.0
December	24/31	59	9	2.5
Sum		3103	547	9.1

pointed localities from Sweden when sorting observations onto maps, gave a total of 4465 reports. The numbers of report strings from August 2013 have been used, as I at this time gained access to the total material from both countries.

Fiure 2. Young, female Great Grey Owl with typical juvenile tail feathers (2CYs). This female was banded as a chick on an artificial breeding platform close to lake Siljan in central Sweden in 2010 and controlled as a breeding bird in Hedmark county, eastern Norway, in 2011.
Ung lappugglehona med karaktäristiska juvenila stjärtpennor (2K vår). Denna hona blev ringmärkt som unge på en boplattform vid Siljan 2010 och kontrollerades som häckfågel i Hedmark, östra Norge 2011.

Results

Of a total sample of 4105 report strings of observed great grey owls, 813 (19.8%) reports included one or more photographs of the observed owl(s). In 323 (39.7%) of these reports at least one of the images (termed +images) could be used for aging the owl. Based on the locality names these photos were judged to portray a minimum of 144 individuals (Table 1).

Of 144 birds, 102 observed in spring had juvenile tail feathers (Figure 2) and these were all 2CY birds from 2011. Another 9 birds were classified as probably belonging to the same age category (Table 3). Only 3 individuals could be aged as 3CY birds, hatched in 2010, while 16 birds were 3CY or older (Figure 3). Two individuals were classified as probably at least 3CY birds. From autumn 2012 there were 10 individuals which were classified as 2CY+, based on their adult tail feathers. Only two of the birds observed in autumn had typically juvenile tail feathers, revealing that they must have been hatched in 2012.

The Swedish species report archives secretariat provided a list of 38 photos accompanying 19 of the restricted reports. While 18 of the photos could not be used for aging, rendering 7 individuals as un-aged, 12 individuals could be aged based on the other 20 images. Of these 9 individuals were 2CY birds, 1 was probably a 2CY bird, while 2 individuals were classified as 3CY+ and 5CY+ birds respectively.

When the report strings from Sweden, downloaded in November 2012 and January 2013 were sorted to monthly reports (tab. 2), March had highest number of reports (810), followed by April (616) and May (504). Uppland and Södermanland topped the list as the landscapes with highest num-

Table 3. Age distribution of Great Grey Owls in Sweden (to landscapes) and Norway in 2012, identified from photos. Photos from restricted reports from Sweden not included.
Ålderfördelning av observerade lappugglor I Sverige (efter landskap) och Norge 2012, identifierade från foton. Foton från skyddade lokaler I Sverige inte medtagna.

Landscape	1CY	2CY	Prob 2CY	2CY+a	3CY	3CY+s	Prob 3CY+s	
Jmtl	0	1	0	1	0	0	0	
Vb	0	1	0	0	0	2	0	
Ång	0	12	0	0	0	1	0	
Mpd	0	19	0	1	1	2	0	
Hsl	0	2	0	0	0	0	0	
Dlr	0	3	1	0	0	1	0	
Gstr	0	5	0	0	0	0	0	
Upl	0	8	0	3	0	1	0	
Srm	1	23	1	0	1	4	1	
Vstm	0	2	1	0	0	0	0	
Nrk	0	3	0	0	0	0	0	
Vrm	0	5	0	1	0	2	0	
Ög	0	1	1	0	0	0	1	
Vg	0	3	1	1	0	0	0	
Dls	0	1	1	0	0	0	0	
Boh	0	1	0	0	0	0	0	
SM	1	2	1	1	0	2	0	
HL	0	0	0	0	0	0	0	
Bl	0	0	1	0	0	0	0	
Sk	0	1	0	1	0	0	0	
Sum	2	93	8	9	2	15	2	
Norway	0	9	1	1	1	1	0	
Sum all	2	102	9	10	3	16	2	144

ber of reports (1059 and 780 respectively; Table 1). A majority of the Great Grey Owls reported from Norway were sighted in the coastal areas from Vest-Agder county to Østfold county, and also in Sweden more observations were reported close to coastal areas (Figure 4).

Discussion

Because the 2CY+ birds from autumn 2012 are non-conclusive as to whether they were hatched in 2011 or earlier, they were excluded from the age distribution comparisons. This means that at least 102 of 134 (76.1%) Great Grey Owls on +images from 2012 were hatched in 2011. When including the individuals classified as probably 2Y birds, there were as many as 111 of 134 birds (82.8%) from 2012 that were hatched in 2011. Stefanssons table 3 (2013) lists 69 Great Grey Owls found dead in 2012 and registered by the Swedish Natural History Museum. In his table 3, 41 of these birds are aged, with 32 as 2CY birds, and 4 as probably 2CY birds. The birds from 2011 thus make up 78.0% of the aged dead birds, and 87.8% when including the four individuals classified as probably 2CY. Thus, the age distribution in my sample of live birds was very similar to that in the sample of dead birds reported by Stefansson (2013).

The high number of young 2CY birds is an obvious result of 2011 being the best breeding year ever for Great Grey Owls in Sweden (Stefansson 2013), and Norway (Berg et al. 2011). Both 2010 and 2011 were however vole peak years on the Scandinavian peninsula, with 2011 as an exceptionally good breeding year for several owl species (Berg et al. 2011, Nyhus & Solheim 2011, Jacobsen et al. 2012). While 2011 was the exceptional Great Grey Owl year in eastern Norway with 22 nests or breeding attempts, both 2010 and 2011 brought high numbers of breeding records in Sweden (77 and 81 nests or breeding attempts; Stefansson 2013). In spite of 2010 being a good breeding year, only 3 of 134 individuals could be classified as 3CY birds in the 2012 reports. Even if we assume that all of the other 3CY+ birds could be 2010-birds, they would maximally make up only 15.7% of the observed

Figure 3. Adult, 3CY+ bird photographed on Tromøya, Aust-Agder county in southern Norway on 14 January 2012. Note the rounded, broad tail feathers with long distance from the outermost dark band to the tip of the feathers.
Adult 3K+ fågel fotograferad på Tromøya, Aust-Agder fylke i Södra Norge 14 januari 2012. Märk de breda, avrundade stjärtpennorna med stort avstånd från det yttre, mörka tvärbandet till fjädrarnas ytterkant.

owls, compared to at least 76.1% 2011-birds. A hypothetical explanation could be that the 2010 birds had lower survival than the 2011 birds. This does not seem very likely, considering the high abundance of voles through autumn 2010 into the breeding season of 2011, which to the contrary ought to give high survival rates of the young hatched in 2010. Another interpretation could thus be that the number of young great grey owls produced in 2011 outnumbered the 2010 generation at least five times. This could very well be the case in the western part of the Great Grey Owl´s distribution range in Scandinavia, as the number of recorded nests or breeding attempts in eastern Norway rose from 3 in 2010 to 22 in 2011 (Berg 2010, Berg et al. 2011). As stated by Stefansson (2013), Great Grey Owls are studied in detail only at a few sites in Sweden, leaving vast forest areas subjected to little or no knowledge of their whereabouts.

It is also possible that young Great Grey Owls behave differently than older birds during food shortage. The congregation of reports from March and April, and close to coastal areas, points to birds hunting voles on snow-free fields close to human settlements. This behavior could indicate that the birds observed had trouble finding enough voles in the forest areas. If older birds are more experienced hunters than young ones, one might expect an overrepresentation of young birds among the observed Great Grey Owls. There is however no reason to assume that older owls are less prone to be killed by traffic than younger birds. The high percentage of 2CY birds among the dead owls from the Natural History Museum in Stockholm (Stefansson 2013) thus supports the interpretation that the population really held a very high proportion of young birds in 2012, since traffic hits make up the majority of mortality amongst these birds. This is in accordance with results found during a winter famine that killed hundreds of tawny owls in southern Norway (Solheim 2006, 2009b), where the proportions of young and older birds were exactly similar in starved and road-killed specimens. Photos of Great Grey Owls from the southern part of Norway during the winter and spring 2011–2012 points to adult birds being as likely as young ones to be observed: of 8 birds, 4 were 2CY, and 4 were older individuals (Solheim unpublished).

The high number of reports from Uppland and Södermanland in Sweden may be caused by high numbers of owls along the eastern coast of central Sweden. However, it may also be explained by the high density of birders in the Stockholm area, with many observers reporting separately on the same individuals. Through the local rarity committees such observations have been lumped together, which made sorting by locality easier in August 2013 than in January 2013.

In Norway a minimum of 63 young fledged from 17 successful great grey owl nests in 2011 (Berg et al. 2011). During winter 2011–2012 no Great Grey Owls were reported seen in the breeding areas of Hedmark county, and remarkably few birds were observed at all in Norway during 2012. Two breeding females controlled in Hedmark county in 2010 and 2011 were hatched on artificial breeding platforms southwest of lake Siljan in central Sweden in 1999 and 2010 respectively (Berg et al. 2011). Because Great Grey Owls have been controlled more than 200 km away from their birth place, it is not unlikely that both old and juvenile birds may have migrated eastwards from Hedmark into Sweden in late 2011, contributing to the high proportion of young 2CY birds reported in Sweden in 2012.

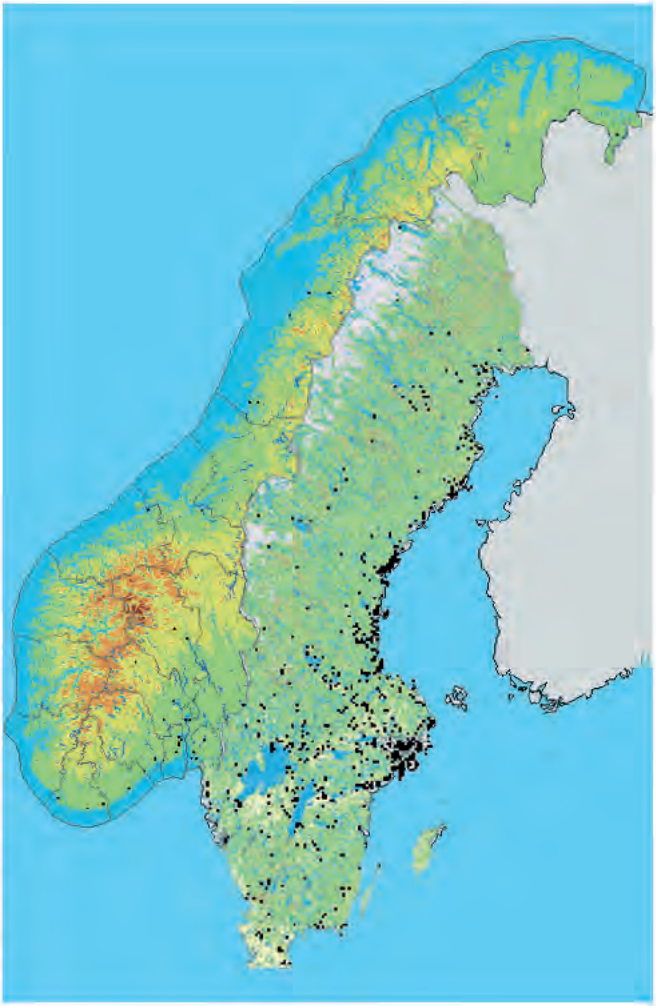

Figure 4. Reports of Great Grey Owls from Norway and Sweden in 2012, as revealed through the mapping command of the national species archives. Maps were presented for each country separately, and had to been stitched together after downloading the images.
Rapporter om observerade lappugglor i Norge och Sverige 2012. Kartor från Artdatabanken i Norge och Sverige. Kartorna kan endast laddas ner från varje land, och är sammankoplade i efterhand.

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Sammanfattning

Lappugglan har under de senaste årtiondena expanderat åt sydväst i hela Nordvästeuropa (Lawicki et al. 2013). I östra Norge är arten en regelbunden häckfågel sedan slutet av 1980-talet (Solheim 2009a), och 2011 var ett rekordår med 22 häckfynd eller häckningsförsök i Hedmark fylke (Berg et al. 2011). Också i Sverige var 2011 ett mycket bra år, med ett beräknat höstbestånd på 4000-4500 individer (Stefansson 2013). Följande år inkom rekordmånga rapporter till Artdatabanken i både Sverige och Norge om observerade lappugglor. De flesta rapporterna kom från Sverige.

Metodik

Hos lappugglor är det tydliga gränser mellan juvenila och adulta ving- och stjärtfjädrar, och ruggningsmönstret kan användas för att ålderbestämma fåglarna, åtminstone efter deras andra vingfjäderruggning (Figur 1, 2 och 3, Solheim 2011). Dessa ruggningsmönster kan också ses på fåglar i fält, och har dokumenterats genom digitalfotografering (Solheim 2009a, 2010, 2011, 2013).

Artdatabanken i Norge och Sverige använder samma databas, utvecklad av det svenska artprojektet som startades 2002. Sökmetodiken är likartad i de två länderna. När rapportörerna dokumenterar sina observationer med digitala foton, kan man hämta ut extra information. Denna studie är ett försök att använda sådan information för att analysera lappugglepopulationens ålderssammansättning under 2012.

Jag laddade ner alla observationer av lappugglor från Sverige och Norge första gången i november 2012 och januari 2013. Denna process upprepades i augusti 2013 eftersom jag efterhand hade fått tillgång till alla observationer i båda länderna. Medan materialet från Norge omfattar 107 enskilda rapporter (varav 49 dolda), var det inte mindre än 4263 enskilda rapporter (varav 265 dolda) från Sverige. I det norska materialet kunde alla dolda rapporter med tillhörande foton hänföras till fyndlokal. I det svenska materialet visade detta sig svårare. I det svenska materialet uteslöts därför de dolda rapporterna. Ålderssammansättningen bland fåglarna i denna lilla del av materialet avviker dock inte från det övriga. Alla rapporter som ledsagades av foton granskades noggrant på en datorskärm med hög upplösning. Alla foton som visade fågelns ålder blev nerladdade för närmare granskning.

Av okänd anledning var antalet rapporterade observationer olika i januari och august 2013. I januari fanns 3103 rapporter som räknades manuellt för att se fördelningen över året (Tabell 2). Rapporterna som laddades ner i augusti 2013 användes slutligen eftersom material från båda länderna var tillgängligt vid denna tidpunkt.

Resultat

Av de 4105 rapporterna ledsagades 813 (19,8%) av ett eller flera foton (Tabell 1). Åtminstone ett fotografi kunde i 323 fall användas för att ålderbestämma lappugglan i fråga. Utifrån lokalitets-id-numren gällde dessa rapporter minst 144 individer, varav åtminstone 102 var 2k-fåglar kläckta 2011. Ytterligare nio fåglar klassificerades som troliga 2k-fåglar, medan tio från hösten 2012 var 2k+ med adulta stjärtpennor. Eftersom dessa fåglar teoretisk kan vara antingen från 2011 eller äldre fåglar, blev de uteslutna vid åldersjämförelsen. Om man inkluderar de möjliga 2k-fåglarna från våren med 2011-fåglarna, utgör denna ålderskategori inte mindre än 82,8% av alla lappugglor som kunde åldersbestämmas 2012.

Störst antal rapporter kom från landskapen Uppland (1059) och Södermanland (780) (Tabell 1). I Norge kom flest rapporter från kuststräckan mellan "fylkene" Vest-Agder och Østfold. Även i Sverige kom flera rapporter från kustnära områden (Figur 4).

Diskussion

Den höga andelen unga fåglar är uppenbarligen ett resultat av att 2011 blev det bästa häckningsåret för lappugglor hittills i såväl Sverige (Stefansson 2013) som Norge (Berg et al. 2011). Medan 2011 var ett framgångsrikt häckningsår i östra Norge med 22 häckningsförsök, var både 2010 och 2011 goda år I Sverige (77 resp. 81 häckningar eller häckningsförsök; Stefansson 2013). Trots detta kunde bara tre av 134 lappugglor med säkerhet bestämmas till 3k-fåglar. Även om man antar att de 16 fåglarna i kategorin 3k+ var från 2010, så utgör denna ålderskategori endast 15,7% av de lappugglor som gick att åldersbestämma. En hypotetisk förklaring på denna låga andel kan tänkas vara att fåglarna kläckta 2010 haft högre mortalitet än fåglarna från 2011. Denna hypotes kan tyckas mindre sannolik då gnagaråret 2010 sträckte sig åtminstone över sommaren och hösten 2011. Ungfåglarna kläckta 2010 borde alltså ha haft mycket goda förhållanden att överleva sitt första levnadsår.

Det är möjligt att ungfåglar har ett annat jaktbeteende än äldre fåglar och oftare samlas på öppna marker nära tätorter när det blir ont om gnagare i skogstrakterna. Det är dock inte troligt att yngre fåglar löper större risk att trafikdödas än äldre fåglar. Av 69 döda lappugglor från 2012 inlämnade till Riksmuseet, kunde 41 åldersbestämmas enligt tabell i Stefansson (2013). Av dessa var 32 ex. säkra 2k-fåglar, och fyra var troliga 2k-fåglar. Bland de döda lappugglorna utgör alltså ungfåglarna minst 78,0%, och möjligen 87,8%. En annan tolkning kan vara att ungproduktionen av lappugglor 2011 var fem gånger högre än föregående år. Detta kan mycket väl vara förhållandet, åtminstone i den västra delen av lappugglans utbredningsområde i södra Skandinavien, då antal kända häckande lappugglor i östra Norge steg från tre 2010 till 22 under 2011 (Berg 2010, Berg et al. 2011). Enligt Stefansson (2013) studeras lappugglans häckning i Sverige endast på några få platser, och det finns mycket stora områden i landet där kunskap saknas om lappugglans förekomst och reproduktion.

Även om minst 63 lappuggleungar blev flygga i 17 framgångsrika revir i Norge 2011, rapporterades förvånansvärt få lappugglor från Norge 2012. Två lappugglehonor som kontrollerats häckande i Hedmark i Norge 2010 och 2011, kläcktes på två olika boplattformar 440 meter från varandra, väster om Siljan 1999 och 2010. Lappugglornas förmåga att på detta vis förflytta sig 200 km eller längre kan mycket väl ha fått alla dessa ungfåglar från 2011 att flyga österut och in i Sverige, och således bidragit till den höga andelen av unga fåglar rapporterade därifrån 2012.

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Difference in population development of Snowy Owl and Great Grey Owl in Fenno-scandia enhance the importance of monitoring both species under a regime of expected future changes of ecosystem cyclicity. Knowledge of population size, reproduction and survival, and age structure of owl populations are important in monitoring these species because reproduction and mortality varies with age.

Snowy Owls and Great Grey Owls can be aged on the pattern of juvenile and adult wing feathers. Bar patterns in the wings can be used to recognise individuals from photos of free flying owls. This is a non-invasive technique which may enhance the amount of data available in population studies of birds.

Photos of Snowy Owls on Beliy Island in Northern Russia in July 2015 showed that 80% of the owls were hatched in 2012-14. 12 Snowy owls satellite tagged in Norway in 2011 spent the summers 2012-14 along the Russian Arctic. This implies that Snowy Owls bred successfully in the Russian Arctic in 2012-14.

The Great Grey Owl expanded as a breeding bird in Hedmark county in 2009-2018. Adult breeding owls were captured for banding or control, and their wings were photographed for moult analyses and aging. Birds which evaded capture were photographed in flight. This method increased the amount of birds which could be aged, especially males. 77% of the recorded breeding Great Grey Owls in 2011 were young birds hatched the previous year. The high number of one year old nesters in 2011 is believed to be a result of natal dispersal from mid-central Sweden following a good reproduction year in 2010.

Data gathered through public sciences were used to age Great Grey Owls. More than 4000 reports of Great Grey Owls observations were registered in the national species archives in Norway and Sweden in 2012. At least 76% of all the Great Grey Owls reported in 2012 were juvenile birds hatched in 2011. This demonstrated that also 2011 was a good reproduction year of Great Grey owls in south Scandinavia.