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Different ecology in male and female wintering Snowy Owls *Nyctea scandiaca* L. in Sweden due to colour and size dimorphism

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Abstract

Wintering Snowy Owls *Nyctea scandiaca* were studied in southern Sweden during four consecutive winters (Nov. - March, 1989 - 1993). 85 % of the known individuals (9-11 males, 11-12 females) in the provinces of Öland and Skåne were considered properly aged and sexed. They were observed for 92 h during daytime roosting and for an additional 29 h during hunting activity. Males were more often mobbed ($p<0.001$) during snowfree conditions, more often roosted in forests ($p<0.01$), left fewer pellets ($p>0.05$), preferred higher perch sites, and stayed shorter periods in the same area ($p<0.01$), as compared to females. First to second winter females were mobbed more often during snowcover compared to bare ground conditions ($p<0.05$), and were mainly selecting medium-sized prey *(Oryctolagus, Anas, Perdix.)* Two older owls (adult female/sub-adult male) were selecting smaller prey *(Microtus, Apodermus, Passerinidae)* compared to first second winter females ($p<0.001$). In conclusion, due to their smaller size and contrasting colouration, males were considered less well adapted to the mainly snowfree conditions in the area, because of a less favourable energy budget due to mobbing, presumed lower hunting success and smaller/less abundant prey. Females, due to their larger size and contrast reducing colouration, were considered better adapted to the same area, due to lower mobbing frequency, presumed higher hunting success and selection of larger prey.

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Introduction

In the Snowy Owl *Nyctea scandiaca* reversed sexual size dimorphism is pronounced. Body masses in the range 1550 – 2690 g have been reported for females, and in the range 1320 – 2013 g for males, from North America (Earhart & Johnson 1970). In this species a sex and age related colour dimorphism also is found, making ageing and sexing possible at most occasions in the field (Josephson 1980, Olsen 1991, Olsen & Fredriksson 1992). Colour and pattern range from almost pure white in the adult male to heavily spotted dark brown in first and second winter females.

Several hypotheses have been put forward to explain the evolution of reversed size dimorphism in raptorial birds: A more efficient (female) nest defense and decreasing vulnerability to predators (Storer 1966, Anderson & Norberg 1981), reduced food competition between the sexes (Earhart & Johnson 1970, Snyder & Wiley 1976, Sylvén 1982, p. 9-19), and (in the Snowy Owl) the advantage of large female size during incubation in cold arctic conditions and the possibility to increase the egg and clutch size (Wiklund & Stigh 1983). Also, the female colouration and pattern could be advantageous because of reduced heat losses through radiation and conduction (Heppner 1970).

Since there is a division of labour between the sexes – only the females incubate, and the males are doing most of the hunting (Tulloch 1969) – the contrast reducing colouration of the females also could reduce the risk of revealing the nest site.

In the Snowy Owl breeding is often associated with dense rodent populations such as voles *Microtus spp.* and lemmings *Lemmus spp.* (Watson 1957, Hagen 1960, Andersson & Persson 1971) and probably also with favourable weather conditions,

since snow sometimes is present for an extended period in the breeding area (Wiklund & Stigh 1986). This results in either nomadism or in that breeding is abandoned in unfavourable years. A juvenile Snowy Owl banded in Canada was recovered in Sakhalin, USSR (Palmerlee 1972), and a juvenile banded in Sweden has been reported from Siberia (Jan Pettersson, pers. com.) suggesting that offspring might search for suitable territories far from the hatching area. Nomadism is still a question of some dispute (Wiklund & Stigh 1986), since adult nonbreeding birds are present for a short period of time in suitable areas during years with shortage of food.

Little is known about the ecology of the species outside the breeding areas. Reports of opportunistic selection of food exists – such as Snowy Owls following aggregations of migrating Willow Grouse *Lagopus lagopus* in arctic Russia (Alerstam 1982, p. 67) – as well as descriptions of several Snowy Owls attracted to a dense population of artifically bred Mountain Hares *Lepus timidus* (Nagell & Fryklund 1965). The food spectrum during the winter also seems wide, and previously described prey species taken by wintering Snowy Owls in Sweden are listed in Table 1 (Levin 1888, Anonymous 1889, Roth 1897, Kolthoff & Jägerskiöld 1898, Anonymous 1904, Nagell & Fryklund 1965).

Regular irruptions of Snowy Owls occur during the winter far south of the breeding range, and previous reports on these invasions (Roth 1896, Nagell & Fryklund 1965, Boxall & Lein 1982, Kerlinger & Lein 1986) describe a predominance of young birds among the individuals found furthest to the south, suggesting differences in winter ecology between different categories of Snowy Owls. Descriptions of females holding exclusive territories during the winter and observations that only females capture larger mammal preys such as Jackrabbits *Lepus* and weasels *Mustela* have been published (Boxall & Lein 1982).

When small numbers of Snowy Owls reached southern Sweden during the winters 1989/90 – 1992/93, this study was designed to evaluate if females as a result of larger size and contrast reducing colouration are better adapted than males to wintering in snowfree areas. The hypothesis was that fe-males are capable of taking larger preys and thus would benefit from a larger spectrum of available prey in areas with few small rodents and more abundant medium sized prey such as rabbits *Oryctolagus cuniculus,* ducks *Anas spp., Bucephala clangula, Aythya spp.* and Partridges *Perdix perdix.* The males, on the other hand, were presumed to be more susceptible to mobbing by birds in snow free areas as a result of smaller size and less contrast reducing colouration.

Table 1. Previously recorded prey species of Snowy Owls during winter in Sweden.

Tidigare registrerade bytesarter för fjälluggla i Sverige vintertid.

Species *Art*	No of sources (references) mentioning the species (out of six) *Antal källor (referenser) som nämner arten (av sex)*
Mammals	
Brown Hare *Lepus europeaus*	1
Mountain Hare *Lepus timidus*	1
Hare *Lepus spp.*	3
Red Squirrel *Sciurus vulgaris*	1
Field Vole *Microtus agrestis*	3
Northern Water Vole *Arvicola terrestris*	1
Bank Vole *Clethrionomys glareolus*	1
Root Vole *Microtus oeconomus*	1
Lemming *Lemmus/Myopus*	1
Wood/Yellow-necked Mouse *Apodemus spp.*	1
Shrew *Sorex spp.*	1
Birds	
Mallard *Anas platyrhynchos*	1
Teal *Anas crecca*	1
Eider *Somateria mollissima*	1
Goldeneye *Bucephala clangula*	1
Coot *Fulica atra*	1
Whimbrel *Numenius phaeopus**	1
Goshawk *Accipiter gentilis*	2
Black Grouse *Lyrurus tetrix*	1
Hazel Grouse *Tetrastes bonasia*	1
Partridge *Perdix perdix*	6
Pheasant *Phasianus colchicus*	1
Green Woodpecker *Picus viridis*	1
Passerines	2

* Might refer to Curlew *Numenius arquata*

Study population and general conditions

The owls included in the study population were observed in southern Sweden, mainly on the island of Öland in the Baltic Sea. Two females observed in Skåne during 1992/93 were also included. These birds made up >85% of all Snowy Owls observed in these areas during the four consecutive winters (Nov – March) of the study. Three observed birds were excluded due to problems with reliable ageing and sexing. These birds were either adult females or first to second winter males.

Thus, my study group contained 2 males and 1 female in the winter 1989/90, 1 male in 1991/92 and 6 – 8 males and 10 – 11 females in 1992/93. In all, 9 – 11 males and 11 – 12 females were included in the analysis. All the males were considered third winter or older (mainly white), one female was judged as adult and the rest of the females first to second winter birds. The study areas were free from snow most of the time, but these conditions were interrupted by short periods when snow covered the ground. Sometimes extensive frost was present, creating a totally white ground similar to snowcover.

Methods

A questionary was distributed to 20 local ornithologists in advance of the winter field observations, asking for information about observation time, habitat, sex, age, other raptorial species in the area, mobbing incidents (mobbing species, number of mobbing individuals and the owl's response). Activity of the owls was noted, as well as choice of roost sites in the day and perch sites (type, height above the ground) during hunting activity. The identity of prey and hunting success or failure were recorded if possible, as well as if and when pellets were produced (if found they were collected). Time spent flying was also recorded, and degree of snow/frost cover was determined.

In addition, announcements were made in the national radio and three major Swedish ornithological journals to gather further information about where owls could be present in the areas. Local and national "birdlines" reporting rare birds were checked every day during the period, and if owls were reported, the observer was interviewed on the telephone shortly afterwards (according to the questionary). In total, Snowy Owls were observed for 92 hours during daytime roosting and for 29 hours during hunting activity at dawn. Half of the observation time was contributed by the author.

Ageing and sexing was made according to Josephson (1980), Olsen (1985) and Olsen & Fredriksson (1992).

Skeletal remains from the pellets were analysed by archeologist Leif Jonsson, Central Board of Natural Antiquities, using the collections at Naturhistoriska Museet, Göteborg, for comparison. Feather remains were analysed by Jan Åkerman, Färjestaden.

Mammal species were named according to Burt (1980) and Macdonald (1993).

Statistics

The bulk of data represents number of observations in various environmental conditions. Comparable observations were made under similar circumstances, and the mean observation times of males and females were almost the same (males: mean 55 min, SD 63.1; females: 64 min, SD 61.3). The data have been subjected to statistical analysis using ordinary statistical tests. Since some expected frequencies were <5, the data were arranged in four-fold contingency tables and observed frequencies were compared with expected ones using Fisher-Irwing's exact test (Armitage 1983). In one instance parametrical data were collected (duration of stay in a winter home range). The values were not normally distributed and, therefore, analysed using Wilcoxon's rank sum test (Armitage 1983).

Table 2. Number of occasions with observations of Snowy Owls at daytime roosting sites. Each observation represents a mean value of 55 min for males and 64 min for females. Males, as compared to females, were mobbed more often during snow free conditions ($p<0.001$) and more often roosted in forested habitat ($p<0.01$). Females were mobbed more often during snowcover as compared to snowfree conditions ($p<0.05$). Statistical test were made by using Fisher-Irwing tests; Armitage 1983.

Antal tillfällen med observationer av fjälluggla på dagsittplats. Var observation representerar i medeltal 55 min (hanar) och 64 min (honor). Hanar mobbades oftare än honor vid snöfria förhållanden ($p<0.001$) och sökte oftare än honor dagsittplats i skog ($p<0.01$). Honor mobbades oftare vid snöiga förhållanden jämfört med snöfria ($p<0.05$). Statistisk analys gjordes med hjälp av Fisher-Irwing test (Armitage 1983).

	Snow absent *Snöfritt*		Snowcover *Snötäcke*		Roosting site *Sittplats*	
	Mobbed *Mobbad*	Not mobbed *Omobbad*	Mobbed *Mobbad*	Not mobbed *Omobbad*	Open *Öppen*	Forest *Skog*
Males *Hanar*	10	12	0	2	18	6
Females *Honor*	1	43	3	7	54	0

Results

Sex-ratio during the invasion 1989 – 1993

The relative number of sub-adult and adult males (45%) was higher than during previously described invasions in Sweden (11%; Anonymous 1889, 15%; Roth 1897, 5%; Nagell & Fryklund 1965).

Mobbing at daytime roosting sites

Males were mobbed more often than first to second winter females ($p<0.001$, Fisher-Irwing test) during snow free conditions. On average, the mainly white males were mobbed once every second hour, the first to second winter females only once in 47 hours. See Table 2.

Females were mobbed more often during conditions with snowcover or frost-white ground ($p<0.05$, Fisher-Irwing test) as compared to snowfree conditions (Table 2). The expected lower frequency of mobbing against males during conditions with white ground could not be verified depending on too few observations. Males were observed for three hours during these conditions and no mobbing incidents occurred. The adult female was never mobbed during 19 hours of observation. Escape flights of the owls as a result of mobbing were recorded only in males, at three occasions. The mobbing was then always carried out by pairs of Ravens *Corvus corax,* presumed to be resident territory holders. After such incidents the owls were not found again in the area. The time spent by male Snowy Owls flying away from mobbing Ravens was 2% of the total observation time during daytime roosting. This is about half as much time as males were observed flying during hunting activity (5%).

Mobbing species are listed in Table 3.

Table 3. Species mobbing Snowy Owls at roosting sites during daytime in winter habitats. Number of observed occasions (with number of mobbing individuals within brackets).

Arter som observerades mobba fjällugglor på dagsittplats i vinterrevir. Antal observationstillfällen med mobbning (samt antal mobbande individer inom parentes).

Mobbing species	Adult/sub-adult male	First/second winter female
Mobbande art	*Adult/sub-adult hane*	*Första/andra vinter hona*
Common Buzzard *Bueto bueto*	–	1(1)
Goshawk *Accipiter gentilis*	1(1 male)	–
Kestrel *Falco tinnunculus*	–	1(1)
Crow *Corvus corone*	3(11)	1(3-4)
Raven *Corvus corax*	6(9)	1(1)

Table 4. Height of perch sites used by four male and nine female Snowy Owls during hunting activity. Number of observations at different perch sites are given.

Höjd för sittplatser använda av fyra hanar och nio honor av fjälluggla under jaktaktivitet. Antal observationer på olika sittplatser anges.

Sex *Kön*	0-1 m	1-5 m	5-10 m	> 10 m
Male	10	10	9	5
Female	34	50	10	–

Choice of daytime roost sites

Only males were found roosting in forests. All females were found in open areas. This difference was significant ($p<0.01$, Fisher-Irwing test; see Table 2). In all, three different males were found on roosting sites in forests. Mobbing frequency was lower in males roosting in forests (17%), than in males roosting in open habitats (50%, $p>0.05$).

Hunting behaviour and choice of perch sites

Hunting behaviour was observed for 3.5 h in four males and for 25.5 h in nine females. In the afternoon, hunting activity was observed more often in adults (5 occasions) than in first to second winter females (1). Hunting individuals used only about 5% of the time flying and the rest of the time perching, usually from the highest point in the section of the habitat selected for hunting activity by the individual. Hovering was rarely seen, and almost exclusively as expected (Sylvén 1978) in hard wind. Flights between perch sites were usually at low altitude, combining gliding and flapping flight.

Males used higher perch sites than females (sites > 5 m above ground, Table 4.) Habitat structure gave no reason to suspect that this was not an active choice made by the individual bird, since trees were occuring in all home ranges studied. On the other hand, no males were reported to hunt along shorelines,

Table 5. Hunting attempts (successful attempts within brackets) made by Snowy Owls where prey could be identified.

Jaktförsök (framgångsrika försök inom parentes) genomförda av fjällugglor där byte kunnat identifieras.

Identified prey *Artbestämt byte*	First/second winter female *Första/andra vinter honor*	Adult female *Adult hona*	Adult male *Adult hane*
Teal *Anas crecca*	1(1)	–	–
Kittiwake *Larus tridactyla*	1(1)	–	–
Herring Gull *Larus argentatus*	1(–)	–	–
Pheasant *Phasianus colchicus*	11(–)	–	–
Partridge *Perdix perdix*	3(1)	–	–
Meadow Pipit *Anthus pratensis*	–	1(–)	–
Passerines	1(–)	–	–
Brown Hare *Lepus europeaus*	3(–)	–	–
Rabbit *Oryctolagus cuniculus*	13(1)	–	–
Vole/Mouse *Microtus/Apodermus*	–	9(2)	>1(?)

Table 6. Prey species identified by skeletal and feather remains in pellets produced by aged and sexed individuals. In addition, one pellet produced by a Snowy Owl of unknown age and sex contained remains from Mallard (1), Partridge (1) and Wood mouse (1).

Bytesarter identifierade från spybollar producerade av ålders- och könsbestämda fjällugglor. Dessutom noterades gräsand (1), rapphöna (1) och mindre skogsmus (1) i en spyboll från en icke ålders/könsbestämd individ.

Prey species *Bytesart*	First/second winter female *Första/andra vinter hona*	Adult female *Adult hona*	Sub-adult male *Sub-adult hane*
Mallard *Anas platyrhynchos*	2	–	–
Teal *Anas crecca*	2	–	–
Goldeneye *Bucephala clangula*	2	–	–
Long-tailed duck *Clangula hyemalis*	1	–	–
Duck *Bucephala/Clangula/Aythya*	1	–	–
Partridge *Perdix perdix*	8	–	–
Starling *Sturnus vulgaris*	1	–	–
Twite/Linnet *Acanthis spp.**	1	–	–
Rabbit *Oryctolagus cuniculus***	5	–	–
Field vole *Microtus agrestis*	3	1	–
Wood mouse *Apodemus sylvaticus*	–	–	2

* Individual with callus-formation in skeletal parts of wing suggesting flight inability when taken.
* *Individ med callusformation i vingskelett som antyder flygoförmåga vid fångsttillfället.*

** All individuals young (<1 yr).
***Alla individer unga (< 1 år).*

though found on daytime roosting sites close to the shore at several occasions. Hunting along shorelines was seen at several occasions in first to second winter (but not in adult) females.

Mobbing during hunting activity at dawn

One female, with a winter territory inhabited also by several Rough-legged Buzzards *Bueto lagopus,* Common Buzzards *Bueto bueto,* Long-eared Owls *Asio otus* and two Goshawks *Accipiter gentilis,* was frequently mobbed by the other birds of prey when hunting at dawn. These incidents usually took place as the owl scared the raptors at their night roosting site or met them on their way to this site. Mobbing incidents during hunting activity at dawn were performed by Rough-legged Buzzard (5), Common Buzzard (1), Goshawk (1 female), Long-eared Owl (1) and Crow *Corvus corone* (2).

Selection of prey and hunting success

Hunting attempts on identified prey species as well as the outcome are presented in Table 5. Prey species identified from pellets produced by known individuals (Table 6) are also listed. Choice of prey of one adult female, lumped with one third to fourth winter male, was compared with the choice of prey of the first and second winter females, regarding type and size of prey. The older owls seemed to prefer smaller prey (voles, mice, passerines) than the younger birds who preferred medium sized prey (rabbits, ducks, part-ridges, gulls, pheasants), ($p<0.001$, Fisher-Irwing test; Table 7). Hunting success at dawn was on average 14%; higher (18%) in attempts by the adult female and lower (13%) in attempts by the first to second winter females ($p>0.05$). In males, hunting success could not be reliably recorded during observations of hunting activity. Hunting success on Öland was also estimated from the number of pellets found on daytime roost sites and frequently used perch sites. Males left only one pellet at 13 inspected sites (9 roosting sites, 4 perch sites) females left 9 pellets in 43 sites (36 roosting sites, 7 perch sites) ($p>0.05$). Because pellets were more often found at perch sites as compared to roosting sites the number given for females might be underestimated.

Since some skeletal parts (the anterior *sternum* marginal, apex of *crista* and *furcula,* but not the *coracoid* seemed to be more abundant in the pellets, a typical (specific?) butchering pattern might be indicated. The skeletal parts found in pellets are examplified in Fig. 1.

Table 7. Selection of food in relation to size of prey in older Snowy Owls (n=2; ≥ third winter) as compared to younger individuals (n=8; first/second winter). Number of prey in the groups small size (voles/mice/passerines) and medium size (hares/rabbits/ducks/partridges/pheasants/gulls) are given. Preys found in pellets as well as identified in the field are included. The difference in food selection between the age-groups is significant ($p<0.001$, Fisher-Irwing test).

Födoval i relation till bytesstorlek hos äldre fjällugglor (n=2; ≥ tredje vinter) jämfört med yngre individer (n=8; första/andra vinter). Antal byten i gruppen små (sorkar/möss/tättingar) och medelstora (harar/kaniner/änder/hönsfåglar/måsar) jämförs. Byten identifierade från spybollar såväl som i fält är inkluderade. Skillnaden i bytesselektion mellan åldersgrupperna är signifikant ($p<0.001$, Fisher-Irwing test).

Age group *Åldersgrupp*	Small size prey *Små byten*	Medium size prey *Medelstora byten*
First/second winter *Första/andra vinter*	6	54
≥ Third winter ≥ *Tredje vinter*	14	0

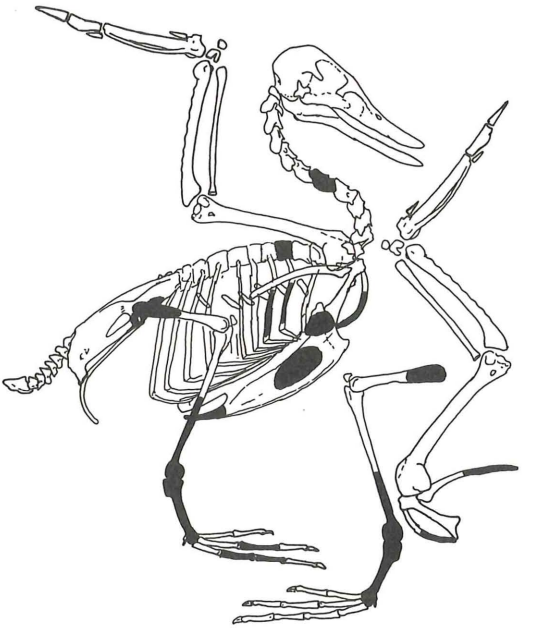

Fig 1. Skeletal parts found in pellets suggest a specific butchering pattern with the prey consumed from the belly side, owls devouring pectoral and leg muscles often leaving head and wings. Given in the figure are the skeletal parts (marked in black) from a Teal *Anas crecca* thought to be representative for medium sized bird preys found in Snowy Owl pellets.

Skelettdelar från spybollar antyder ett arttypiskt slaktmönster där bytet konsumeras från buksidan varvid ugglan förtär bröst- och benmuskler och ofta lämnar vingar och huvud. I figuren visas skelettdelar (svärtade) från en kricka Anas crecca *som bedöms vara representativa för medelstora fågelbyten funna i spybollar från fjälluggla.*

Territoriality, home range and duration of stay

Whether or not territoriality exists in wintering Snowy Owls could not be verified. A congregation of owls observed in 1993, consisting of one adult male, one adult female and four first to second winter females were studied for two weeks. Frequently the owls were seen sitting ten to fifty meters from each other during the days, without any signs of aggression. However, at dawn they usually separated. At one occasion a first winter female, approaching the hunting area of the adult male, was fiercely and repeatedly attacked by the male until she left the area where the male continued to hunt.

Size of home ranges in the temporary winter habitat could not be determined at most observation points since the owls continued their hunting during darkness (when they could not be observed). However, a first to second winter female present for more than three months in the same area, were never seen outside a 5 km^2 area.

The duration of stay in the same winter home range was shorter for males (median: 3 days, range: 1 – 18) than for females (median: 23 days, range: 3 – 106), ($p<0.01$, Wilcoxon rank sum test). Mean time for males found to use concealed daytime roost sites (n=3) were slightly longer, 8.0 days, than for males found only in open habitats (n=6), 3.3 days ($p>0.05$).

Discussion

This study shows a greater susceptibility to other mobbing birds (especially pairs of Raven) for the smaller and mainly white males compared to the more spotted and larger females during snowfree conditions (Table 2). This aspect of the winter ecology of the Snowy Owl is not previously reported on, and might be a part of the explanation why adult males are found wintering further to the north than younger females. Other explanations, social dominance of the larger females over males, have previously been given (Kerlinger & Lein 1986) to this distribution of different age and sex classes in wintering Snowy Owls.

Female Snowy Owls, as compared to males, were shown to be mobbed mostly when active at dawn, when colouration was presumed to be of less importance. In the females, during daytime observations, mobbing increased significantly (Table 2) in conditions with white ground as compared to bare ground, which is in support of less negative effects of mobbing in snowfree winter habitats.

Mobbing frequency also might be one of the explanations to the selection of more concealed roosting sites during the day in males, where they were mobbed less frequently. Also, only males were losing energy as a result of escape flights due to mobbing. This suggests that mainly white males are less well adapted to snowfree conditions, especially if pairs of Ravens are present. If balancing on a tight energy budget, this loss of energy could be of negative importance to the individual.

Boxall & Lein (1982) found in Alberta, Canada, that only female Snowy Owls seemed to be able to take larger mammals such as Whitetail-jackrabbits *Lepus townsendi* and Long-tailed Weasels *Mustela frenata*. This could not be cleraly verified in this study, but the single pellet produced by the studied males could possibly indicate a food niche of smaller prey species. Also, during the observations of hunting activity males made fewer hunting attempts as compared to females, and no prey species could be identified during the observations (Table 6). This may indicate lower hunting success and/or preference for smaller prey species in the males. The shorter time spent in a winter home range area for the males could then be a result of a less favourable energy budget compared to first and second winter females.

The first to second winter females selected larger prey species than the two older individuals studied (Table 7). It is doubtful, though, if the difference is age or sex related.

Boxall & Lein (1982) found that only females were territorial, defending a home range during the winter. Males were staying for shorter periods, perhaps as a result of competition with the larger females. The only incident with intraspecific aggression during this study does not support this suggestion, since the adult male successfully defended the hunting area against a larger young female. The agility seemed to favour the male. In support of this observation is a study of nest defence by Snowy Owls in Sweden (Wiklund & Stigh 1983). The nest sites were almost invariably defended most aggressively by the male, whereas females used distraction behaviour. The shorter periods spent by males in the same area, found in Alberta, Canada, (Boxall & Lein 1982), as well as in this study, could possibly be a result of a different food budget for males (smaller and/or less abundant prey species). Energy loss depending on escape flights could then have had a more pronounced negative effect on the males.

In the Snowy Owl the insulation efficiency of the plumage is extremely high. According to Gessaman (1972), the thermal conductance is as low as 0.05 cal/g/h, which corresponds to the conditions in the fur of the Arctic Fox *Alopex lagopus* during the winter. A lower conductance (0.041 cal/g/h) has been found only in one bird species tested, the Adelie Penguin *Pygoscelis adeliae*. In spite of this fact, Snowy Owls must increase their consumtion of Lemmings from 2 – 4 during the breeding period to 4 – 7 during winter conditions to maintain their weight (Gessaman 1972). This indicates the great importance of the energy budget. The preference for higher perch sites found in the males (Table 4), therefore might reflect a selection of more wooded habitat not only for shelter, but also in search for areas with more dense populations of small rodents than the soil-thin steppe-like ("alvar-areas") and shores that females used most often. However, a similar interspecific distribution of low and high perch sites was found in a study of sympatrically wintering buzzard species in Sweden (Sylvén 1978). In the latter case, selection of prey of the two species was almost identical, with the only exception of *Apodemus spp.*, taken more often by the higher perching Common Buzzard than the Rough-legged Buzzard. Interestingly, *Apodemus sylvaticus* was the content of the only pellet of male origin in this study.

Females, in contrast to males, did never perform escape flights caused by Ravens, and they were never found in forested areas when hunting at dawn or roosting during the day. Evidence of a food spectrum consisting of mostly medium sized preys such as rabbits, ducks, partridges were found in first to second winter individuals. Mobbing was less pronounced during snowfree conditions (Table 2), which also might be advantageous during the brooding (less risk of exposing the nest site) since this is probably due to the females contrast reducing colouration during snowfree conditions. This is indicative of a better adaptation to the environment studied. They also stayed longer and left more pellets (n=22).

In conclusion the results of this study favour the idea of a difference in winter ecology between (older) males and (younger) females of Snowy Owl

Snowy Owls on bare and snowy ground. Males (previous page) are much easier to detect without any snow on the ground whereas a female (above) has a colouration that makes her less easy to detect. Photo: H. Rigbäck (upper left) and H. Persson.

Fjällugglor på barmark och i snö. Hanar (föreg. sida) är mycket lättare att upptäcka på barmark medan honan (ovan) har en färgteckning som gör henne mindre lätt att upptäcka.

as a result of reversed size dimorphism and intersexual difference in colouration.

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Sammanfattning

Olika ekologi hos hanar och honor av fjälluggla under övervintring i Sverige beroende på färg- och storleksdimorfism

Fjälluggla *Nyctea scandiaca* är en art med uttalad könsdimorfism. Honan har i genomsnitt ca 30% högre kroppsvikt (Earhart & Johnsson 1970). Färgteckningen hos arten varierar från närmast helvit (adult hane) till kraftigt mörkfläckig på vit botten (uttalat hos yngre honor). Många hypoteser har framlagts för att förklara evolutionen av omvänd könsdimorfism hos rovfåglar och ugglor: ett mer effektivt boförsvar (honor) och minskad känslighet för predatorer (Storer 1966, Andersson & Norberg 1981), ökad gemensam födonisch för paret (Earhart & Johnsson 1970, Snyder & Wiley 1976, Sylvén 1982), samt (för fjälluggla) fördelen av större vikt hos honan vid ruvning under arktiska förhållanden samt möjligheten att öka ägg- och kullstorlek (Wiklund & Stigh 1983). Det mörkfläckiga mönstret på vit botten hos honor har angetts ge minskade värmeförluster till omgivningen (Heppner 1970, Wiklund & Stigh 1983).

Häckning hos fjälluggla är associerad med samtidig hög täthet i gnagarpopulationer (Watson 1957, Hagen 1960, Andersson & Persson 1971). Om arten är nomadisk är inte övertygande visat (Wiklund & Stigh 1986). Boungar från Kanada och Sverige har återfunnits i Sibirien (Palmerlee 1972 m.fl.). Adulta fåglar förekommer dock korta perioder under häckningssäsongen i lämpliga områden även år då häckning ej kan ske p.g.a. för små bytespopulationer (Wiklund & Stigh 1986).

Artens vinterekologi är mindre känd. I Ryssland följer dock fjällugglor ansamlingar av sträckande dalripor *L. lagopus* (Alerstam 1982) och i Sverige har ansamlingar noterats i ett område med artificiellt uppfödda skogsharar *Lepus timidus* (Nagell & Fryklund 1965), talande för ett opportunistiskt födoval. Tidigare beskrivna bytesdjur i Sverige vintertid är noterade i Tabell 1. I Nordamerika återfinns ungfåglar av båda könen söder om adulta fåglar vintertid (Kerlinger & Lein 1986). Enbart honor har här rapporterats försvara vinterrevir (Boxall & Lein 1982) och slå medelstora däggdjur *(Lepus, Mustela).*

Syftet med min vinterstudie var att testa hypotesen om honor har kapacitet att ta större byten och är mindre känsliga för mobbande fåglar och därför bättre i stånd att erhålla en god energibudget i områden med få smågnagare (*Apodemus, Microtus* m.fl.) och fler medelstora byten som fåglar (*Anas, Perdix* m.fl.) och kaniner *Oryctolagus*, främst under snöfria förhållanden.

Metodik

Fåglar som uppträdde vintertid under någon av fyra på varandra följande vintrar i Skåne och på Öland inkluderades då ålders och könsbestämning kunde anses säker. Totalt inkluderades 10 – 11 yngre (första och andra vinterdräkt) honor, 1 adult hona och 9 – 11 sub-adulta/adulta hanar under 1989 – 1993. Snöfria förhållanden dominerade under perioden.

Ett frågeformulär distribuerades till ca 20 lokala ornitologer. Via detta samlades information om ugglans ålder, kön och beteende. Även mobbningincidenter, sittplatsval, jaktbeteende, bytesval, framgång vid jakt, observationstid, relativ flygtid och grad av snötäckning m.m. noterades. Spybollar insamlades. Totalt observerades fjällugglor 92 timmar dagtid och ytterligare 29 timmar under jaktaktivitet. Ålders- och könsbestämning gjordes främst enligt Josephson (1980). Statistisk analys med Fisher-Irwings exakta test och Wilcoxons ranksummetest genomfördes enligt Armitage 1983.

Resultat och diskussion

Könskvoten inom den studerade populationen avvek (45% sub-adulta/adulta hanar) från tidigare rapporter från Sverige (5 – 15%) vintertid.

Under snöfria förhållanden mobbades övervägande vita hanar signifikant oftare dagtid ($p<0.001$) än yngre honor, Tabell 2. Yngre honor mobbades signifikant oftare dagtid vid snötäcke jämfört med barmark ($p<0.05$), Tabell 2. Mobbning som ledde till att fjällugglor utnyttjade energi för att undkomma flygande noterades enbart hos hanar. Mobbningen utfördes då parvis av (förmodligen revirhållande) korpar. (Efter sådana episoder återsågs ingen hane inom samma vinters home range). Ugglehanar utnyttjade 2% av observationstiden dagtid till att flyga undan mobbande korp, jämfört med under jaktperioden i skymningen, då 5% av observationstiden ägnades åt flygaktivitet.

Hanar valde signifikant oftare sittplats i skog än honor ($p<0.01$) och mobbades där mindre ofta än i öppna områden (Tabell 2).

Jagande individer observerades oftast i skymningen, men hos främst adulta individer ibland även under eftermiddagen. Jaktflykten skedde oftast < 1 m över marken och kombinerade aktiv flykt med glidflykt. Ryttling noterades sällan och som förväntat (Sylvén 1978) mest i hård vind. 95% av tiden spanade ugglorna efter byte. Hanar valde högre spaningspunkter än honor, Tabell 4.

En yngre hona mobbades vid flera tillfällen vid jakt i skymningen. Detta skedde oftast då den stötte andra rovfåglar från nattkvist eller mötte dem på väg till densamma.

Data för jaktförsök, framgångsrika jaktförsök samt spybollsmaterial presenteras i Tabell 5 & 6. En subadult hanes och en adult honas bytesval jämfördes statistiskt med yngre honors. Signifikant fler ($p<0.001$) medelstora byten (*Anas, Perdix, Oryctolagus*) togs av de yngre honorna, Tabell 7. Andel framgångsrika jaktförsök var 14% hos honor, (hanar icke bedömningsbara). Jaktframgång i form av andel funna spybollar på mer frekventerade sittplatser var högre ($p>0.05$) hos honor (21%) än hos hanar (8%).

Dagtid förelåg inga tecken på hävdande av vinterrevir. En ansamling av sex fjällugglor inom 2 km radie studerades under ca 14 dagar. Ofta satt flera ugglor (av olika ålders och könsklasser) bara tio till femtio meter från varandra utan tecken till aggres-

sion. En adult hane försvarade vid ett tillfälle i skymningen framgångsrikt ett jaktområde mot en större yngre hona med dykningar och slag av klor mot huvud/rygg. Definitiv storlek av jaktområde kunde ofta inte fastslås eftersom jakten i allmänhet fortsatte efter mörkrets inbrott. Tidsperiod som en och samma individ stannade inom samma home range var signifikant längre för honor än hanar ($p<0.01$). Hanar stannade 1 – 18 dygn (median 3), och honor 3 – 106 (median 23).

Det huvudsakliga fyndet vid denna studie förefaller vara att huvudsakligen vita fjällugglehanar mobbades signifikant mer än yngre honor (dagtid under snöfria förhållanden). Detta är möjligen inte rapporterat tidigare, men kan vara en av förklaringarna till varför adulta fjällugglor övervintrar mer nordligt. Yngre honor mobbades signifikant oftare vid snö än barmark, och mest av allt i skymningen när färgteckning misstänktes ha mindre betydelse. Detta antyder att äldre hanar kan vara mindre väl anpassade till snöfria övervintringsområden. Att denna högre mobbningsfrekvens kan ha betydelse för individen styrks av att enbart hanar noterades på dagsittplats i skogsmiljöer, där mobbningsfrekvensen också var lägre. Att hanar förlorar energi till följd av flykt undan mobbande korpar kan ha betydelse för individen, speciellt om dess energibudget är snäv. I studien noterades att flykt undan korpar dagtid motsvarade ca hälften av den tid hanar använde till flygaktivitet under jakt. Vidare antyder resultat från studien (innehåll i spybollar, frekvens funna spybollar samt jaktstudier) att hanarna sannolikt har en annan födonisch med mindre byten, främst små gnagare. Eftersom smågnagare inom det studerade området sannolikt också är sällsyntare än medelstora byten, förefaller det som om flera faktorer gemensamt talar för en snävare energibudget för hanar. Energiförluster till följd av mobbning skulle därför i verkligheten kunna ha en viss negativ betydelse och vara en orsak till att hanar stannade kortare perioder i området. Att denna separation i val av byte mellan hanar och honor verkligen föreligger stöds också av en studie från Alberta, Kanada, där enbart honor kunde visas slå större däggdjur som harar (*Lepus*) och större vesslor (*Mustela*) (Boxall & Lein 1982). En liknande signifikant skillnad mellan födoval för två subadulta/adulta fåglar jämfört med honor i första och andra vinterdräkt noterades i vår studie (Tabell 7). Om denna skillnad var köns- eller åldersberoende är dock oklart.

I Boxall & Lein's studie visades också att enbart honor försvarade vinterrevir (social dominans av större individer), ett argument som använts för att ange varför ungfåglar återfinns söder om äldre och hanar söder om honor i Nordamerika om vintern (Kerlinger & Lein 1986). Den enda incidenten i min studie av intraspecifik aggression stöder dock inte helt denna rapport, eftersom en (äldre) hane framgångsrikt försvarade sitt jaktområde mot en (yngre) hona, vilket möjligen inte rapporterats tidigare.

Hos fjällugglan är isolationen i fjäderdräkten mycket hög, värmeförlusterna är 0.05 kal/g/timme, detta motsvarar värmeförlusterna i fjällrävens vinterpäls (Gessaman 1972). Trots det måste fjällugglor öka sin dygnskonsumtion av lämmlar från 2 – 4 under häckningstiden till 4 – 7 vintertid för att hålla vikten (Gessaman 1972). Detta understryker energibudgetens betydelse för övervintrande fjällugglor. Att hanar i min studie oftare spanade från högre punkter under jakt i skymningen kan vara ett uttryck för selektion av ett annat jakthabitat. Trädrikare miljöer inom uggleindividens home range kan ha valts av hanarna inte bara som skydd från mobbning dagtid, utan också för att dessa miljöer sannolikt är rikare på smågnagare än jordfattiga alvar och stränder.

Honor, till skillnad från hanar, flög aldrig undan för mobbande fåglar och blev aldrig funna i skogiga miljöer under jakt eller dagtid. De mobbades mindre frekvent, speciellt under snöfria förhållanden, vilket också kan vara en fördel vid boet (mindre risk att avslöja boplats). I min studie kunde också visas att yngre honors födospektrum främst består av medelstora byten som fåglar (*Anas, Bucephala, Perdix*) och kaniner (*Oryctolagus*) under vintern. De lämnade också fler spybollar och kan ha haft högre jaktframgång. Dessa faktorer talar gemensamt för en bättre adaption till studerat habitat, medan hanar av samma orsaker föreföll sämre anpassade till detta övervintringsområde.

Sammanfattningsvis talar resultaten för en skillnad i vinterekologi för (äldre) hanar jämfört med (yngre) honor som en effekt av omvänd storleksdimorfism och skillnad i färgteckning mellan könen.