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Moult and breeding of captive Northern Hawk Owls *Surnia ulula*

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During 2003–07, the moult of four captive Northern Hawk Owls *Surnia ulula* was studied in Poznań Zoological Garden (Poland). The aviary was under daily observation and all breeding events were recorded. It was recognized that captive conditions differ from that in the wild (food availability, expended energy – especially by males, and stress) but the study of captive owls allowed a detailed study of moult in relation to the breeding cycle of Northern Hawk Owls. Identification of dated moulted feathers enabled us to reconstruct the moult process of primaries, secondaries and rectrices. During this study the four birds had different breeding status: single, paired without breeding, paired with unsuccessful or successful breeding. In nine cases, the moult corresponded to patterns described in literature. In every case all primaries and rectrices were renewed each season. Males started moulting 3–11 days earlier than females and shed all secondaries every year while females replaced from 50–100% of secondaries annually. Rate of moult was not related to ambient temperature. During a successful breeding season, the moult of both sexes was two-phased: a short first phase with low moult intensity lasting until young owlets left the nest box followed by a longer, more intense second phase. Breeding females (egg laying and incubation) started to moult a few weeks earlier than non-breeding females but completed moult at approximately the same date. In contrast, breeding and non-breeding males had similar patterns of moulting intensity.

Key words: Northern Hawk Owl, *Surnia ulula*, moult, captive breeding, energy trade-off, ecological constraints

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INTRODUCTION

In many birds, moulting, breeding and migration usually do not overlap within the annual cycle (Payne 1972, Hahn *et al.* 1992, Kjellen 1994). All these activities are nutrient and energy demanding so their temporal separation provides ecological benefits. According to Payne (1972), daily energy demands of moulting birds are 5–30% higher than within the rest of the annual cycle. That increase is the result of higher protein demands for new feather growth and reduced thermoregulatory ability. According to Payne (1972), overlap of moulting and breeding may occur in two situations: when food is abundant all year, or when food is only seasonally abundant during the breeding season and there is a shortage of food during the rest of the year. Energetic constraints influence the timing of moulting and breeding in owls, which metabolise much of the body fat reserves during the breeding and moulting season (Hardy *et al.* 1982). Most European owl species postpone moult until after or close to the end of the breeding season. As a consequence, reproducing birds moult later than non-breeders (Pietiainen *et al.* 1984, Hirons *et al.* 1984, Petty 1994).

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The Northern Hawk Owl *Surnia ulula* seems to have a less common strategy with a relatively early moult period which overlaps the breeding period (Forsman 1980, Cieślak & Kwieciński 2005). Rather than waiting to moult after young have fledged, this species start an energy consuming moult while in the progress of feeding its young. However little is known about the exact timing of shedding feathers and about energy costs of replacing feathers in this species. Only Forsman (1980) provided initial data on the moult pattern in Northern Hawk Owls, based on museum material and captured wild owls. Some data based on museum specimens of North American subspecies *Surnia u. caparoch* are available in Pyle's (1997) monograph. We decided therefore to study moult patterns in captive Northern Hawk Owl (Cieślak & Kwieciński 2005). The aim of this paper was to investigate when birds moult in relation to the breeding cycle. We did this by daily records of moult progress in captive owls and relating these to the stage of breeding.

Relatively little information is available on European owl's moult in relation to their breeding ecology. Studies of owls living in captivity (zoos, bird rehabilitation centres) could provide information on aspects of ecology more easily and in more detail than similar studies in the wild (Pyle 1997). Obviously, differences in ecological conditions in captivity and the wild should be taken into consideration when results are interpreted.

METHODS

The study was conducted in the Poznań Zoological Garden (western Poland) in 2003–07, on two pairs of Northern Hawk Owls (Table 1). The first pair (F1 and M1) was born in 2002 and successfully bred in 2003. In 2004 the first clutch was destroyed by an unknown predator (2 chicks were killed and the incubated eggs were abandoned by the female). After 12 days, the female started to lay another clutch of six eggs, but before these eggs hatched she stopped incubation. A detailed description of the moult pattern in this year was given in Cieślak & Kwieciński (2005). In 2005 the pair incubated successfully but soon after hatching the male and four of the chicks died from aspergillosis. In 2006 and 2007 female F1 was single. The second pair (F2 and M2) was born in 2005 and bred for the first time in 2007 when incubating 9 eggs and raising 5 young. The owls were housed in standard aviaries (25 m^2) with nest boxes (35 x 35 x 45 cm) and were exposed daily to zoo visitors. Food (mice) and water were provided daily *ad libitum*. Owls cached surplus of mice in small holes in the walls.

Daily food consumption was recorded annually for female F1, for male M1 only in 2004 and for female and male F2 and M2, respectively, only in 2006. The mean daily food intake was calculated on the basis of the difference between the weight (g) of the food provided and that left uneaten. Ambient temperature data during the moulting period were recorded by the Poznań Institute of Meteorology.

From April to August, aviaries and nest boxes were inspected every day to collect moulted feathers (primaries, secondaries and rectrices). Two innermost secondaries (s16 and s17) were ignored in this study due to their small size. Feathers were identified by shape and length. To help identify the position of secondaries in the wing (their ordinal numbers) these feathers were individually marked the previous autumn (Fig. 1). See Appendix 1 for an example of the records collected per individual. Three indices were used to describe and measure moult.

Table 1. Number of captive Northern Hawk Owls investigated and their breeding status.

Year	Breeding status Pair 1[a]	Breeding status Pair 2[b]	Number of birds
2003	7 eggs / 2 young raised	-	2[c]
2004	9 eggs / 2 young lost 6 eggs lost	-	2
2005	9 eggs / 2 young raised[d]	-	1
2006	Single female	No breeding	3
2007	Single female	9 eggs / 5 young raised	3

[a]Male M1 and female F1, born in 2002.
[b]Male M2 and female F2, born in 2005.
[c]No daily moult scores.
[d]Another four young and the male died at the beginning of June after mycotic infection (aspergillosis).

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Figure 1. Photograph of open Northern Hawk Owl wing showing method of marking (indicated by the arrows) the position of secondaries in the wing during autumn moult verification.

Intensity of shedding index (ISI) describes how often and how long feathers are shed in a given period or over the whole moulting season. It is the ratio of total length of shed feathers to number of days and is expressed in mm/d. The length of shed feathers were derived from an owl feather database where average length of primaries, secondaries and rectrices was calculated on the basis of 24 feather sets (MC, unpubl. data). This index was used to investigate the effect of ambient temperature on feather shedding patterns.

Number of feathers growing simultaneously was another parameter describing the intensity of growing new feathers. It was based on our 2004–05 measured feather growth rate of 5 mm/d. We assumed that all feathers grow at the same rate from start to end of their growth period as supported by photographs of Northern Hawk Owl open wings. Based on moult summary data (Appendix 1) the number of feathers growing simultaneously each day was calculated for the period starting when the first feather was shed and until the last shed feather had finished growing.

Annual secondaries exchange index (AISE) was used to evaluate the extent of feather replacement during the moulting season. This index was applied only to secondaries since all the primaries and rectrices were replaced annually. The AISE value was calculated as a ratio of the sum of length of replaced secondaries to the sum of length of all secondaries (s1 to s15) multiplied by 100 (expressed as a percentage). For example, female F1 in 2003 did not replace four secondaries in her left wing (s4, s7, s8, s9) and three secondaries in her right wing (s4, s7, s8) giving an ASEI value of 75.1%. The length of feathers used to calculate the index was derived from an owl feather database (MC, unpubl. data). Throughout the year, the timing of all elements of the breeding cycle (eggs laying, incubation, fledging) were recorded.

The number of feathers growing simultaneously was analysed by a mixed model (SPSS 14.0), which accounts for repeated measurements. Individual birds were entered as subject in the analysis with year, sex and breeding status (breeding or not) as fixed factors. Means are reported ± SD.

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RESULTS

Moult pattern

Each individual replaced all primaries and rectrices annually. In all four male cases, all secondaries were replaced regardless of breeding status (Table 2). In seven female cases, all secondaries were replaced (ASEI = 100%) only once by non-breeding female F2 in 2006. Female F1's ASEI came close to 100% in 2004 when her breeding attempts failed. The ASEI for the remaining five female cases ranged from 50% to 79%.

Food consumption and ambient temperature

Mean daily food intake during the moulting period ranged from 130.6 ± 32.1 g to 163.9 ± 15.8 g for female F1 (recorded annually), and was 138.0 ± 21.7 g for female F2 in 2006. Mean daily food intake was 131.4 ± 31.6 g for male M1 in 2004 and 130.0 ± 31.6 g for male M2 in 2006. Mean ambient temperature during moulting seasons was: 15.7 ± 4.18°C in 2004, 15.4 ± 5.0°C in 2005, 17.9 ± 5.0°C in 2006 and 15.8 ± 5.0°C in 2007. Ambient temperature and rate of moult were in most cases not correlated (Table 3).

Table 2. Annual secondaries exchange indices (ASEI) of captive Northern Hawk Owls. Breeding years are bold.

Year	Annual secondaries exchange index (%)			
	Pair 1		Pair 2	
	F1	M1	F2	M2
2003	**75.1**	**100**	-	-
2004	**92.8**	**100**	-	-
2005	**50.3**	-	-	-
2006	64.2	-	100	100
2007	64.3	-	**79.0**	**100**

Moult vs. breeding

On average, the number of simultaneously growing feathers was 14.1 ± 8.85 (Fig. 2). The number of growing feathers was significantly lower in breeding individuals than in non-breeding individuals ($F_{1,1103}$ = 14.98, $P < 0.005$). There were no differences among years although the year effect approached significance ($F_{3,1102}$ = 2.54, P = 0.055). Males and females did not differ in the number of feathers moulting simultaneously ($F_{1,1102}$ = 0.07, P = 0.79). The apparently less intensive moult in breeding birds compared to non-breeders concurred with a longer time period needed to complete moult (131 days and 112 days, respectively) but sample sizes were too small to draw firm conclusions (n_{total} = 9, $F_{1,7}$ = 2.30, P = 0.17). Breeders started on average 15 days earlier in time than non-breeders but completed moult at the same time (difference 0.5 day).

Figure 2 compiles all observations on numbers of simultaneously growing feathers for each individual throughout each breeding season. Non-breeding females replaced feathers in a clear uni-modal pattern. In contrast, breeding females exhibited two distinct phases of moult; first a short and less intensive phase, followed by a second phase that lasted for a longer time and during which more feathers were replaced simultaneously. Breeding birds started to shed feathers while still incubating the eggs. Before the last chick hatched, both males and females shed the four or five innermost (and shortest) primaries and males shed four very short inner secondaries (for moult order see Appendix 1). Just after the last chick left the nest box the second phase of intensive moult began. Through about the first 10 days of this phase, the number of growing feathers increased slowly, but later rapidly increased due to moult of 12 long rectrices in a relatively short period (4 to 11 days by breeding females, and 8 to 19 days by breeding males). A long period of many simultaneously growing feathers during the sec-

Table 3. Spearman rank correlation of the rate of moult and daily ambient temperature in four captive Northern Hawk Owls.

Bird	2004	2005	2006	2007
F1	r_s = 0.217, n = 106, P = 0.025	r_s = –0.052, n = 94, P = 0.619	r_s = –0.050, n = 73, P = 0.677	r_s = 0.011, n = 56, P = 0.935
F2	-	-	r_s = 0.181, n = 102, P = 0.071	r_s = 0.304, n = 104, P = 0.002
M1	r_s = 0.176, n = 104, P = 0.075	-	-	-
M2	-	-	r_s = 0.177, n = 126, P = 0.053	r_s = 0.158, n = 112, P = 0.098

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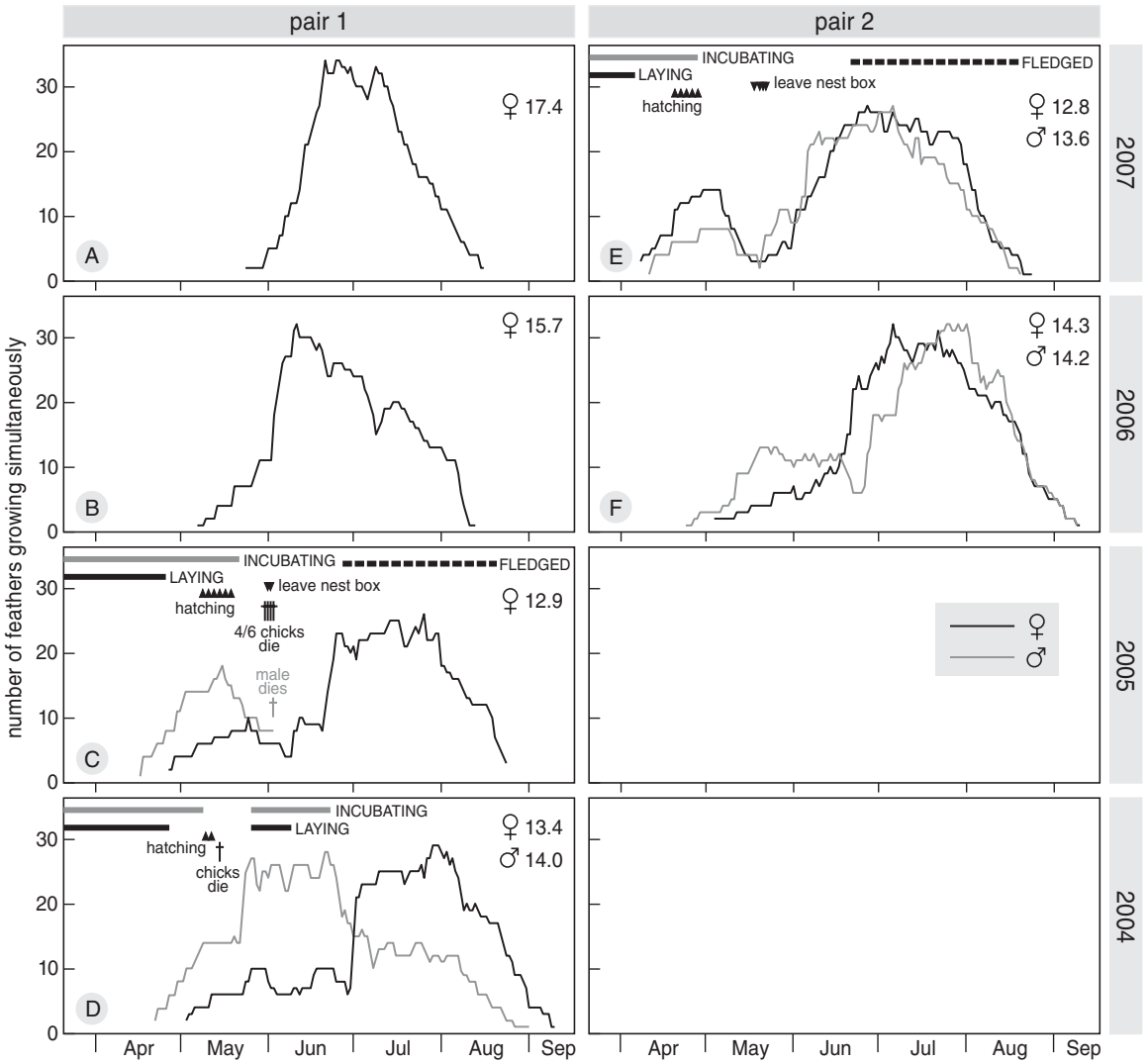


Figure 2. Daily numbers of feathers growing simultaneously for each of the individual captive Northern Hawk Owls in successive years. Average values for each individual are given. For breeding pairs the different stages of breeding are indicated. In 2004, chicks and eggs of the first clutch of pair 1 were lost, and the second clutch was abandoned after almost four weeks of incubation. In 2005, four of the six chicks and the male died due to aspergillosis.

ond phase was the result of growing long rectrices, long outer primaries and many outer and middle secondaries (Fig. 2, Appendix 1). Males followed roughly the same pattern as females but tended to replace more feathers during the early moult period.

DISCUSSION

Our results generally support earlier observations that the Northern Hawk Owl exhibits a considerable overlap in moult and reproduction (Forsman 1980, Cieślak & Kwieciński 2005). In breeding females the moult progressed in two distinct phases. During the first approximately 15% of the feathers were replaced. A second phase began when the young left the nest and in the period that the young were fed by the parents a further 28% of the feathers were replaced (Fig. 2), which underlines the considerable amount of overlap between moult and reproduction.

Possible costs of moult were reduced by moulting fewer feathers at the same time than non-breeders did. Moreover, beginning the moult early with relatively short feathers allowed the owls to reduce the number

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of simultaneously growing new feathers during the energetically demanding period when young owls are growing fastest (3–4 weeks old). The moult order at the beginning of the moult cycle exhibited by the Northern Hawk Owl and many other bird species seems to be evolutionarily optimised to use time-limited energy resources for both moulting and reproducing.

The strategy of an early moult suggests a trade-off to optimally use the high prey availability during the brief spring and summer periods of the Nordic landscape for both breeding and moulting. The pattern observed can be explained by the food situation that the species encounters. Because small mammal prey availability vary considerably in location and over time (rodent cycles), Northern Hawk Owls are forced to disperse nomadically after breeding and moulting to search for food resources to survive the forthcoming winter. The need to overlap moult and breeding periods has selected for breeding strategies that optimize the use of available resources for reproduction and new feather growth simultaneously. One element of such trade-off mechanism in the Northern Hawk Owl is a variable clutch size (3–13 eggs) which is dependent on food resources in a given year (Mikkola 1983). Reduction of clutch size in poor food years accommodates the energetic demands of moulting.

Another element of this strategy is the early start of the female's moult just after the energy demanding egg-laying stage (Fig. 2). The male's contribution to reproduction at that stage of the breeding cycle (foraging for its mate and himself) is less energetically demanding, so males can moult earlier (3, 10 and 11 days in our birds). But the intensity of the first moult phase in both sexes during the first stages of breeding was relatively low compared to the second phase of moulting (Fig. 2).

To cope with the short time periods when food is abundant many owls collect a surplus of food and store (cache) it for later use in more demanding periods. The captive owls we studied also cached mice during the first phase of moult despite being provided with food *ad libitum* suggesting that caching behaviour is an innate strategy that has evolved under natural selection. Cached food resources are crucial for the Northern Hawk Owl's strategy of moulting during the breeding season (Huhtula *et al.* 1987). In the wild, 4–5 week old owlets are not independent and must be fed by their parents with lowered flight and hunting ability. Cached food probably helps the flight-challenged moulting parents feed young owlets while they learn to hunt.

Specific features of the Northern Hawk Owl's moult strategy is that breeding females accelerate their moult by about 15 days earlier than non-breeding females (Fig. 2) including a relatively early and almost simultaneous moult of rectrices, the growth of which is supported by cached food. By late summer, when owlets are independent, parents with new plumage are ready for long nomadic flights to find scarce prey during winter. In contrast, Forsman (1981) found that in some years when a captive Spotted Owl *Strix occidentalis* laid and incubated infertile eggs they moulted nearly a month later than in years when it did not nest.

The Northern Hawk Owl has an advanced annual moult, replacing up to 100% of all primaries, secondaries and rectrices. A dynamic flyer, it is diurnal with a rather large hunting territory. It also preys on flying birds especially during the non-breeding period. After one season of use, feathers of wild Northern Hawk Owls sometimes look badly worn. It is thus very important for this species to maximize the extent of feather moult annually to maintain optimal flying ability for hunting during the critical winter period. Also, other diurnally active owl species that hunt birds in flight (Little Owl *Athene noctua*, Eurasian Pygmy Owl *Glaucidium passerinum*), thus suffering a relatively quick wear of the feathers, show a more advanced annual rate of feathers exchange (Schönn *et al.* 1991, Cieślak & Kwieciński, unpubl. data). In contrast, nocturnal owls that hunt by ear and pounce on terrestrial prey (Tengmalm's Owl *Aegolius funerus*, Barn Owl) have less extensive annual moult (Piechocki 1961, 1974, Lenton 1984, Hornfeldt *et al.*, 1988, Cieślak & Kwieciński 2006).

The comparison of the moult intensity of breeding and non-breeding females (Fig. 2) helps understand the complex physiological relationship between breeding and moulting (Payne 1972). We speculate that the hormonal reactions of female Northern Hawk Owls during the initial phase of the breeding cycle could also stimulate an earlier start of moult. Such stimulation may also affect intensity of moult. This conclusion is supported by a high value of the annual secondaries exchange index (ASEI) by female F1 in 2004 when she laid two clutches (total 15 eggs; Table 2).

Female F1's moult in 2005 (low ASEI value of 50%) may have been influenced by the aspergillosis infection which killed her mate M1 and their four chicks, even she did not show any visible symptoms of illness. The lower ASEI values for female F1 during her 'widow' years (2006 and 2007) support our thesis on the significance of the role of breeding hormones in the stimulation of feather moult intensity, but annual moult rates or intensity may also decrease with age as reported for others owls (Eurasian Eagle Owl *Bubo bubo*, Mebs in

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Glutz von Blotzheim & Bauer 1980). To address this question we plan to continue our study by providing a new mate for female F1.

The brood loss observed in 2004 coincided with a different moult pattern of both owls (F1 and M1) that differed than that observed when breeding was successful. Female F1 displayed a prolonged first phase of moult (up to about 60 days) that included the laying and incubation of a second clutch. The delayed start of female F1's second phase of intensive moult illustrated the relationship of moulting and breeding. The Male M1's moult in relation to the observed brood loss is difficult to explain. The rapid increase of moult intensity just after this event could either be result of a lack of young to feed or associated with the stress associated with breeding failure.

Effect of captive conditions

The main differences between wild and captive Northern Hawk Owls that might influence the observed relationship between moult and breeding include food availability and diversity, energetic (flight) demands for hunting and nest defence, feathers abrasion rates (collisions with aviary walls and ceiling), disturbance (human visitors), photoperiod and zoogeographical/climatic factors (the owls we studied were observed far away from their natural breeding range). These differences may have influenced the results we observed and must be considered in extrapolating our conclusions to wild birds. But a species' evolved strategies and mechanisms do not necessarily disappear in captivity. Payne (1972) concluded that the phenology of moult in captive birds was consistent with that of wild birds. Also, we documented that owl food caching behaviour persisted in captivity even when food was provided *ad libitum* suggesting that this is an innate behaviour.

According to Forsman (1980) and Cramp (1988), Northern Hawk Owls in the wild seldom replace all secondaries each season. We documented that captive owls moulted these feathers more intensively – with four of 11 cases in which birds replaced all their secondaries. This was likely the result of increased food availability and lower energy demands. The lower annual rate of secondaries replaced by breeding females supports this thesis. Comparisons with the reported moult patterns of wild Northern Hawk Owl (Forsman 1980, Pyle 1997) we conclude that captive conditions do not significantly modify the moult (sequence and order of moulted feathers) and phenology relative to the breeding cycle. Better food availability and lower energy expenditures probably increased the rate of annual feather exchange, confirming the conclusions of other authors (Nero & Copland 1997, Hornfeld *et al.* 1988). The lower energy expenditure (reduced flight for hunting) by captive males could result in increased annual rate of feather exchange (ASEI) comparing to captive breeding females and wild males.

In the wild, breeding success is influenced by food availability and weather (Cramp *et al.* 1988, Newton 1998, Taylor *et al.* 1992). Our results show that in captivity moult rate is not related to ambient temperature, perhaps because in captivity temperature (and other elements of weather) does not influence the availability of food. Others have concluded that the rate of moult and weather-influenced food availability are related (Cramp 1988, Newton 1998, Korpimäki 1992, Sondell 2000). We conclude that while captive conditions may have influenced our research results we nevertheless were able to document in detail an interesting relationship between breeding and moult in the Northern Hawk Owls that would be almost impossible to achieve with birds in the wild.

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SAMENVATTING

In de jaren 2003–07 werd het ruipatroon van vier Sperweruilen *Surnia ulula* onderzocht in de dierentuin van Poznań, Polen. De vogels werden dagelijks geobserveerd en de broedcyclus werd in detail vastgelegd. Waarnemingen aan gekooide vogels zijn niet zonder meer toepasbaar voor vogels in het wild, maar daar staat tegenover dat gedetailleerde gegevens moeilijk zijn te verkrijgen in veldsituaties. Alle geruide veren werden verzameld, zodat de rui van handpennen, armpennen en staartveren kon worden onderzocht. De vier vogels verschilden gedurende de onderzoeksperiode in broedstatus: ze waren ongepaard, gepaard zonder te broeden, gepaard en broedend maar zonder succes, of gepaard en succesvol broedend. In negen gevallen kwam het ruipatroon overeen met beschrijvingen in de literatuur. De hand- en staartpennen werden ieder jaar vernieuwd. Mannetjes begonnen 3–11 dagen eerder dan vrouwtjes te ruien en ze vervingen ieder jaar alle armpennen. Bij vrouwtjes was meer spreiding in het ruipatroon, waarbij soms alle armpennen werden vervangen en soms maar de helft. De snelheid van de veergroei was gecorreleerd met de voedselopname, maar niet met de omgevingstemperatuur. Wanneer de vogels succesvol een broedsel grootbrachten, verliep de rui van beide seksen in twee fases. Eerst een korte fase, waarbij weinig veren tegelijkertijd werden geruid, die duurde tot de jonge uilen het nest verlieten. Daarna een tweede fase die langer duurde en waarbij meer veren tegelijkertijd werden vervangen. Vrouwtjes met nest en eieren ruiden enkele weken eerder dan niet-broedende vrouwtjes. Er bestond bij mannetje echter geen verschil tussen broedvogels en niet-broedvogels.

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Appendix 1. Moult pattern of non-breeding female Northern Hawk Owl F2 during season 2006. Numbers illustrate simultaneous shedding of given feathers on both sides within 1–2 days, letters L (left) and R (right) illustrate 3 days and longer shedding asymmetry. Bold numbers illustrate shading dated on the basis of one-side feather found (one feather omitted and not collected, but verified as replaced).

	Primaries										Secondaries															Tail-feathers					
	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	1	2	3	4	5	6
2 May										L																					
10									R																						
15									L																						
23								3																							
30							R																								
3 June							L																								
6–7						5																									
9																								L							
10																							L								
12																								R							
15																							R								
16					6																				15						
18																														L	L
20																												3	4	R	R
22																						12									
26				R																							R				
27																											L				
28				L																											
30																										1					
2 July											L				5						L										
3											R																				
4			8																		R										
7																															
12		R																													
13		L																		L											
16																				R											
17																L															
20	10															R															
23												R	R																		
24												L																			
25													L																		
26																			R												
1 Aug																			L												
2																	R														
5																	L														
7																		8													
9														L																	
11														R																	

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ARDEA

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