

Moult in Tawny Owls *Strix aluco* in Relation to Food Supply and Reproductive Success

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ABSTRACT

1. The number of flight feathers (rectrices and remiges) moulted annually in Tawny Owls was investigated by dye-marking feathers one year, before moult commenced, and recapturing the owls in the following year. The recaptures of 214 females and 91 males from a forest in northern England were used in the analyses.

2. There was considerable variation in the number of wing feathers moulted annually. Males moulted slightly more feathers than females but the differences were not significant. The median number of primary feathers moulted annually for males and females was 6 and 4 respectively out of a total of 20. For secondary feathers it was 10 and 9 respectively for males and females out of 26.

3. Wing feather moult was significantly related to breeding success. Birds that did not breed moulted most feathers, while those that reared the largest broods moulted fewest.

4. Breeding success of Tawny Owls was significantly related to a three-year cycle of Field Vole abundance. Therefore, because moult was related to breeding success, it was also indirectly related to vole abundance. The result was that Tawny Owls moulted most wing feathers in years of low vole abundance, when most did not breed, and fewest in years of high vole numbers (increasing and decreasing vole year classes) when most pairs bred.

5. Tail feather moult was not related to breeding success, or to any other factor investigated. Most birds replaced all twelve tail feathers biennially. Usually all feathers were replaced in the same year, but in a minority of birds a variable number of feathers were replaced each year, although individual feathers were only replaced every two years.

6. The reasons for the evolution of different moulting strategies for feather tracts are discussed. All body feathers were replaced annually and this may be crucial to prevent heat loss. The moult of wing feathers can be deferred for one, two or even more years. This suggests that in a perch hunter like the Tawny Owl, the condition of wing feathers is less important than tail feathers which are maintained in better condition by a biennial moult. Tail feathers are probably more important for steering Tawny Owls when they drop from perches onto prey.

INTRODUCTION

The replacement of feathers is necessary for both efficient insulation and flight (for reviews see Payne 1972; King 1980). Most passerines undergo a complete annual moult whereas many larger, longer-lived birds replace body feathers annually but may defer the replacement of flight feathers for two or more years. Because additional energy and protein are required for feather growth, most temperate species moult either before or just after breeding, or during a lull in the breeding cycle when energy demands for these purposes are reduced.

The Tawny Owl *Strix aluco* is a sedentary, nocturnal predator of small mammals (Mikkola 1983; Cramp 1985). Its moult is complex and has been described in some detail by Piechocki (1961, 1968), Stresemann & Stresemann (1966), Glutz & Bauer (1980), Hardy *et al.* (1981), Ginn & Melville (1983), Hirons *et al.* (1984) and Cramp (1985). There are considerable differences between most of these accounts.

In this paper I present data from individually known Tawny Owls which were caught during each nesting attempt when their remiges (primary and secondary feathers) and rectrices (tail feathers) were dye-marked at each capture to check the progression of moult. There were significant annual differences in numbers of wing and tail feathers moulted related to reproductive success. The main food of Tawny Owls in the study area was the Field Vole *Microtus agrestis* which exhibited a three-year cycle of abundance (Petty 1987a). In low vole years, few pairs of Tawny Owls even laid, and those that did produced small broods. In both increasing and decreasing vole years a high proportion of Tawny Owls bred and successfully reared chicks (Petty 1989).

STUDY AREA

The study was undertaken in the central part of Kielder Forest, Northumberland in northern England (55°N, 2°W). In the study area the forest comprised largely Sitka Spruce *Picea sitchensis* and Norway Spruce *Picea abies* grown on rotations of 45–55 years. The forest was entirely man-made. Afforestation commenced in 1933, while clear-felling and replanting (restocking) commenced in 1968. By 1991 there was an extensive patchwork of first and second generation tree crops developing, particularly at lower elevations where the initial planting took place.

METHODS

Moult was studied during 1985–1990. In this period the Tawny Owl population increased from 54 to 66 occupied territories. Most of the Tawny Owls bred in nestboxes (Petty 1987b). Female owls were caught at the nestbox with a hand-held net similar in shape to a butterfly net. Male owls were caught in a trap which was placed over the entrance to the nestbox. The trap was a modification of that described by Saurola (1987). Most breeding females were caught each time they bred during 1985–1991 and males during 1988–1991. Female and male owls were caught when the oldest chick was 5–15 days old.

The presence of active flight feather moult (growing feathers) was checked in each owl caught during the incubation and nestling periods. Tawny Owls have 10 primary and 13 secondary feathers in each wing and 12 tail feathers. The first time a bird was caught, part of the white area on the underside of these 58 feathers was permanently dyed yellow with picric acid in a solution of 70% alcohol plus a wetting agent. During subsequent recaptures the position of any new feathers (undyed) was recorded and the feather dyed.

Owls were not always caught every year, but providing they were caught every second year, then feathers moulted in the first or second year could be identified by looking at the white basal area on the underside of the primary and secondary feathers. Feathers replaced on the last moult had a pink/brown wash to this white area while those replaced on the previous moult had faded to white. It was not possible to do the same with tail feathers, so the sample sizes for tail moult analysis were smaller than for primary and secondary feathers.

Two reproductive parameters from the owls were used in the analysis. Brood size was the number of chicks leaving the nest site. Pairs which failed to rear chicks could be classed either as

those which laid and then failed during the incubation or the nesting period, or those which failed to lay altogether. The start of incubation was used to measure the timing of breeding (Petty, unpublished).

The analyses treat each annual moult record from an owl independently, although moult data from the same individual but in different years were used.

The population of Field Voles exhibited a pronounced three-year cycle of abundance (Petty 1989; Petty unpublished). Years were classified according to vole populations as low (1986, 1989) increasing (1987, 1990) or decreasing (1985, 1988).

RESULTS

Timing of moult

In 226 owls that were recaptured during the nesting period none out of 62 males was moulting. In 164 females, one bird had six primaries partly-grown, one had two secondaries partly-grown and five had one secondary partly-grown. None had active tail moult. Moult mainly commenced in both sexes once the chicks had left the nest site in May-June, as evidence came from the presence of moulted flight feathers found in the territory. Therefore, most birds caught during a breeding attempt had not started their annual moult.

Number of flight feathers moulted annually

There was considerable variation in the number of flight feathers moulted annually (Table 1). A surprising number (17-19%) of owls replaced no primary feathers at all in a particular year, while very few (1-6%) replaced all 20. Males appeared to moult slightly more primary feathers at each moult than females (Table 1), but there was no significant difference between the sexes in the median number of feathers moulted annually (Mann-Whitney U-test, $z=-1.179$, $p>0.05$).

In contrast to the moult of primary feathers, very few owls failed to moult some secondary feathers, but none moulted all 26 (Table 1). Again males appeared to moult slightly more secondaries than females (Table 1), with no significant difference between the sexes in the median numbers of feathers moulted ($z=-0.903$, $p>0.05$).

The pattern of tail feather moult was quite different to that of wing feathers. Most owls moulted either none or all 12 tail feathers (Table 1). This was because tail feathers were replaced in total every second year in most owls (see later).

What influences the number of flight feathers moulted?

Variation in the annual replacement of wing feathers was related to breeding success. Birds that failed to lay moulted most primary and secondary feathers, while those rearing the largest broods moulted fewer (Table 2). The number of wing feathers moulted by males and females showed a similar significant relationship with breeding success. However, in males the number of chicks reared (1-4) was progressively associated with a decrease in the number of wing feathers moulted, particularly primaries. In females, however, the number of wing feathers moulted showed less variation with brood size (Table 2 and Figure 1).

Breeding success in Tawny Owls was related to vole abundance (Petty 1987a and 1989), so understandably wing feather moult but not tail moult was also related to vole abundance (Table 3). There were great similarities between the sexes in the numbers of primary, secondary and tail feathers moulted in each vole year class (low, increasing or decreasing). Males moulted slightly more primary and secondary feathers than females (Table 3). In low vole years significantly more primary and secondary feathers were moulted than in other vole year classes. In increasing and decreasing vole years there were no significant differences in the numbers of primary feathers moulted (Table 3), but significantly fewer secondaries were moulted in decreasing than in increasing vole year classes.

The number of primary feathers moulted in a given year was positively related to the number of secondary feathers moulted (males $r=0.72$, $df=90$, $p<0.001$; females $r=0.64$, $df=213$, $p<0.001$). Hence, moulting more primaries did not lead to a decrease in the number of secondaries moulted.

Table 1. The number (%) of flight feathers moulted annually by Tawny Owls in Kielder (1985-1990). Each owl has 12 tail feathers, 20 primary and 26 secondary feathers (both wings).

Number of feathers moulted	Primaries		Secondaries		Tail	
	female	male	female	male	female	male
0	40 (18.7)	15 (16.5)	3 (1.4)	0 (0.0)	38 (23.3)	22 (30.1)
1	25 (11.7)	6 (6.6)	1 (0.5)	0 (0.0)	15 (9.2)	6 (8.2)
2	13 (6.1)	7 (7.7)	7 (3.3)	4 (4.4)	6 (3.7)	8 (11.0)
3	18 (8.4)	2 (2.2)	7 (3.3)	3 (3.3)	14 (8.6)	5 (6.9)
4	12 (5.6)	9 (9.9)	11 (5.1)	5 (5.5)	11 (6.8)	1 (1.4)
5	10 (4.7)	4 (4.4)	12 (5.6)	8 (8.8)	3 (1.8)	1 (1.4)
6	8 (3.7)	6 (6.6)	14 (6.5)	7 (7.7)	2 (1.2)	0 (0.0)
7	8 (3.7)	3 (3.3)	23 (10.7)	5 (5.5)	4 (2.5)	2 (2.7)
8	6 (2.8)	4 (4.4)	14 (6.5)	8 (8.8)	8 (4.9)	1 (1.4)
9	6 (2.8)	5 (5.5)	19 (8.9)	2 (2.2)	10 (6.1)	3 (4.1)
10	12 (5.6)	5 (5.5)	13 (6.1)	4 (4.4)	9 (5.5)	6 (8.2)
11	7 (3.3)	3 (3.3)	10 (4.7)	4 (4.4)	13 (8.0)	3 (4.1)
12	8 (3.7)	1 (1.1)	10 (4.7)	5 (5.5)	30 (18.4)	15 (20.6)
13	3 (1.4)	3 (3.3)	5 (2.3)	3 (3.3)		
14	7 (3.3)	3 (3.3)	12 (5.6)	4 (4.4)		
15	5 (2.3)	0 (0.0)	10 (4.7)	4 (4.4)		
16	9 (4.2)	4 (4.4)	6 (2.8)	4 (4.4)		
17	5 (2.3)	3 (3.3)	10 (4.7)	4 (4.4)		
18	5 (2.3)	3 (3.3)	11 (5.1)	2 (2.2)		
19	4 (1.9)	0 (0.0)	5 (2.3)	4 (4.4)		
20	3 (1.4)	5 (5.5)	7 (3.2)	1 (1.1)		
21			4 (1.9)	6 (6.6)		
22			0 (0.0)	1 (1.1)		
23			0 (0.0)	1 (1.1)		
24			0 (0.0)	1 (1.1)		
25			0 (0.0)	1 (1.1)		
26			0 (0.0)	0 (0.0)		
Number of owls	214 (100)	91 (100)	214 (100)	91 (100)	163 (100)	73 (100)
Median number of feathers moulted	4	6	9	10	4	3

Table 2. The mean number of flight feathers moulted annually in Tawny Owls in relation to sex and brood size, Kielder 1985-90.

Brood size	Primary feathers				Secondary feathers				Tail feathers		
	Mean	n	SE	RT	Mean	n	SE	RT	Mean	n	SE
Female											
NB	13.17	48	0.69	D	15.69	48	0.57	B	6.60	25	1.08
0	8.56	16	1.23	C	11.82	16	1.48	AB	7.36	11	1.56
1	5.06	17	1.28	ABC	9.18	17	1.18	A	5.77	13	1.49
2	5.72	46	0.81	BC	8.33	46	0.63	A	5.63	38	0.80
3	2.54	52	0.42	A	7.85	52	0.53	A	5.04	43	0.65
4-5	3.40	35	0.67	AB	8.71	35	0.73	A	4.94	33	0.76
ANOVA	F=33.24, p<0.001				F=21.86, p<0.001				F=0.77, p>0.05		
Male											
NB	13.67	21	1.00	D	18.00	21	0.90	B	6.18	17	1.34
0	10.86	7	2.25	CD	12.43	7	2.74	AB	10.00	4	1.68
1	9.38	8	2.19	ACD	11.13	8	1.44	A	5.57	7	1.78
2	5.96	23	1.14	ABC	9.09	23	1.13	A	3.44	16	1.00
3	3.04	25	0.58	AB	7.84	25	0.80	A	4.04	23	1.03
4-5	1.43	7	0.54	A	8.57	7	2.17	A	6.00	6	2.42
ANOVA	F=16.40, p<0.001				F=12.05, p<0.001				F=1.60, p>0.05		

Brood size = number of chicks fledging; NB = not breeding; 0 = birds which laid but failed to rear any chicks.
RT = Scheffe range test (95%); similar letter denotes no significant difference.

Table 3. The mean number of flight feathers moulted annually in Tawny Owls in relation to sex and vole year classes, Kielder 1985-90.

Vole year class	Primary feathers				Secondary feathers				Tail feathers		
	Mean	n	SE	RT	Mean	n	SE	RT	Mean	n	SE
Female											
1	12.84	58	0.65	A	14.50	58	0.63	A	5.86	35	0.87
2	3.95	102	0.43	B	9.77	102	0.46	B	5.24	93	0.47
3	4.09	54	0.61	B	6.59	54	0.44	C	6.37	35	0.85
ANOVA	F=79.67, p<0.001				F=46.10, p<0.001				F=0.78, p>0.05		
Male											
1	13.37	30	0.88	A	16.40	30	0.97	A	5.30	23	1.06
2	4.42	37	0.76	B	10.27	37	0.78	B	4.72	36	0.79
3	4.38	24	0.83	B	6.13	24	0.77	C	5.43	14	1.54
ANOVA	F=40.39, p<0.001				F=32.99, p<0.001				F=0.14, p>0.05		

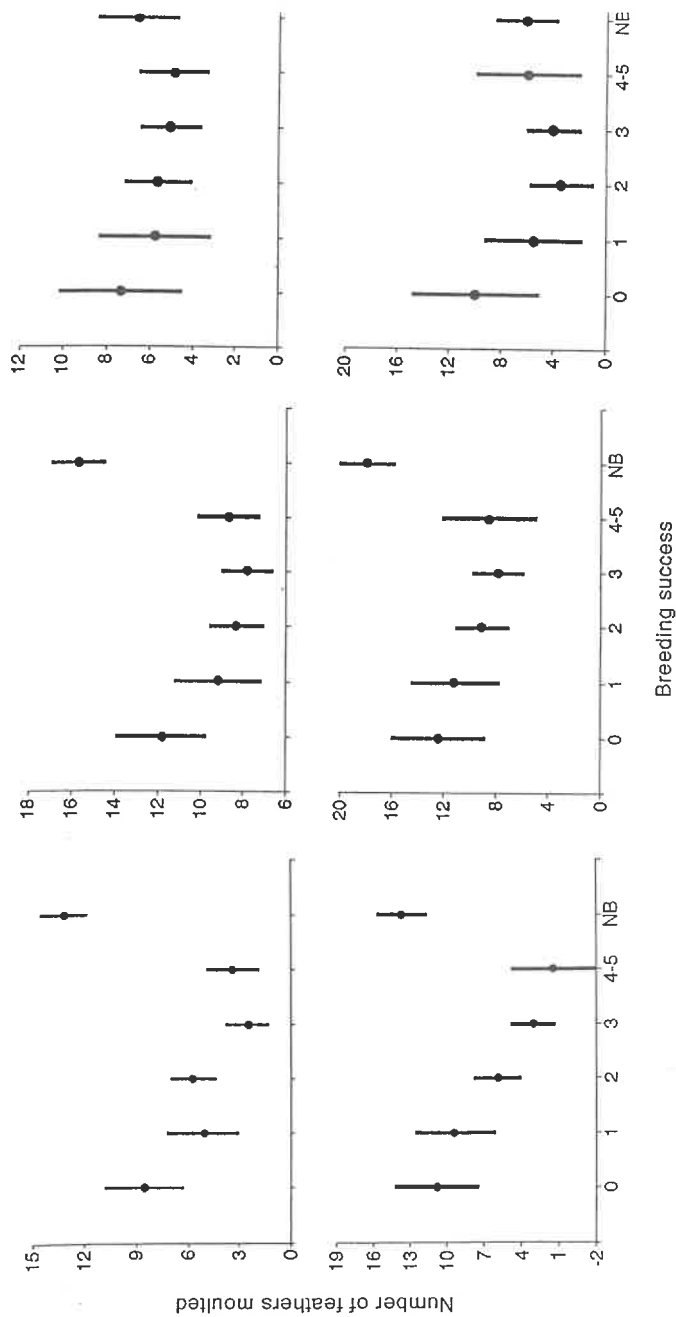
Vole year class: 1 = low, 2 = increasing, 3 = declining
RT = Scheffe range test (95%), similar letter denotes no significant difference.

Table 4. Moults of two female Tawny Owls (ring numbers GJ73197 and GH40939) through their first five and six annual moult cycles. Both owls were ringed as nestlings.

Bird number	Age *	Wing	Primaries										Secondaries													Tail												
			1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	
1	1	L	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	J	J	J	J	J	J	J	J	J	J	J
1	1	R	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	N	N	N	N	N	N	N	N	N	N
1	2	L	J	J	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	N	N	N	N	N	N	N	N	N
1	3	L	J	N	N	N	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	O	O	O	O	O	N	O	N	N	O	O	O	O
1	3	R	J	N	N	N	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
1	4	L	N	O	O	O	N	N	O	O	O	O	N	N	O	N	O	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
1	4	R	N	O	O	O	O	N	N	O	N	N	N	N	N	O	N	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
1	5	L	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	O	O	O	O	O	N	X	O	N	N	O	N	O	
1	5	R	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N		
1	6	L	O	N	N	N	O	N	O	N	O	O	O	O	N	N	O	O	N	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
1	6	R	O	N	N	N	O	N	O	O	O	O	O	O	N	N	O	O	N	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N		
2	1	L	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	J	J	J	J	J	J	J	J	J		
2	1	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	N	N	N	N	N	N	N	N	N	
2	2	L	J	J	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	N	N	N	N	N	N	N	N	
2	2	R	J	J	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	N	N	N	N	N	N	N	N	
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2	3	R	N	N	N	N	O	O	N	N	J	J	J	J	N	N	J	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
2	4	L	O	O	O	O	O	O	O	O	N	N	N	N	O	N	O	O	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
2	4	R	O	O	O	O	O	O	O	O	O	N	N	N	O	N	O	O	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N		
2	5	L	O	O	O	O	N	O	O	O	O	O	N	N	O	O	N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
2	5	R	O	O	O	O	N	O	O	O	O	O	N	N	O	O	N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
2	6	L	N	N	N	N	O	N	N	N	N	N	N	N	O	N	N	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N		
2	6	R	N	N	N	N	O	N	N	N	N	N	N	N	O	N	N	O	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N		
2	7	L	O	O	O	O	N	O	O	O	O	O	O	N	O	O	N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
2	7	R	O	O	O	O	N	O	O	O	O	O	O	N	O	O	N	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	

* Age: 1 = prior to the first adult moult in the second year of life, 2 = after the first adult moult and prior to the second adult moult in the third year of life, etc.
 J = juvenile feather; N = new adult feather grown during the last moult; O = old adult feather not replaced at the last moult; X = feather missing.
 Primary feathers are numbered outwards from the body, secondary feathers inwards towards the body and tail feathers from left (1) to right (12).

Figure 1. The mean (with 95% confidence limits) number (y axis) of wing feathers moulted annually in relation to breeding success (x axis) by Tawny Owls in Kielder. Breeding success scores are; 0 = eggs laid but no chicks fledged, 1-4 = number of chicks fledging, NB = no breeding attempts. The left-hand figures are for primaries, the centre ones for secondaries and the right-hand ones for tail feathers. The upper graphs are for females and the lower ones for males.



In contrast, there was no relationship between the number of tail feathers moulted and breeding success (Table 2), vole year type (Table 3) or total wing feathers moulted (males $r=0.14$, $df=72$, $p>0.05$), (females $P=0.01$, $df=162$, $p>0.05$). Nor could I find any other factor related to tail feather moult.

All twelve juvenile, tail feathers were replaced on the first adult moult in the second year of life (Table 4). All yearlings (31 females and 30 males) caught prior to their first adult moult had complete juvenile tails. In contrast, all two-year olds (13 females and 18 males) caught before their second adult moult had complete adult tails. All three- and four-year old owls also had complete adult tails.

DISCUSSION

Moult of body feathers

Although this study did not specifically consider the moult of body feathers, the evidence indicates body feathers are replaced annually (Witherby *et al.* 1940; Stresemann & Stresemann 1966; Glutz & Bauer 1980; Cramp 1985).

Tawny Owls are extremely well feathered, even the legs and toes have a dense cover. This is probably an adaptation to conserve heat during periods of inactivity, particularly during cold weather. Therefore it is essential that body feathers should be kept in prime condition. The only way to do this is to replace them annually.

Moult of wing feathers

Most previous reports of wing feather moult in Tawny Owls suggest that all feathers are replaced annually (Piechocki 1968; Hardy *et al.* 1981; Ginn & Melville 1983; Hirons *et al.* 1984), whereas some continental studies suggest that wing feather moult is rarely completed each year (Stresemann & Stresemann 1966; Glutz & Bauer 1980).

My study demonstrates clearly that the number of wing feathers moulted was closely related to breeding success, which in turn was related to food abundance. Tawny Owls fed largely on Field Voles, which had a pronounced three-year cycle of abundance. Most Tawny Owls bred and reared broods in years when vole populations were increasing or decreasing. In these years relatively few primary and secondary feathers were moulted, presumably due to the high energy demands of rearing chicks.

After leaving the nest, young Tawny Owls are dependent on their parents for about three months (Southern *et al.* 1954; Southern 1970; Petty & Thirgood 1989). So juveniles do not become independent until mid to late August, and most adult owls have finished moulting by the end of September (Hirons *et al.* 1984).

Moult requires energy and is often associated with a substantial reduction in locomotory activity (Wijnandts 1984). Tawny Owls with dependent young cannot afford to reduce locomotory activity, and thus moulting is delayed until late August. Once their offspring have dispersed, little time is left for moulting and it may be essential for their own survival to channel surplus energy into replacing body feathers rather than wing feathers.

Primary feathers provide forward propulsion while the secondary feathers provide lift. So, a perch hunter like the Tawny Owl may not be heavily dependent on its wing feathers being in perfect condition for efficient prey capture. Therefore, energy is more appropriately channelled into breeding rather than spent on wing feather replacement. In contrast, Sparrowhawks *Accipiter nisus* are more agile aerial hunters which are dependent on the efficiency of their wing feathers, and replace all their primary and most secondary feathers annually (Newton & Marquiss 1982). Unlike Tawny Owls, female Sparrowhawks commence their wing and tail feather moult during incubation at a time when energy requirements are low. This ensures that enough time is available to replace all wing feathers before the autumn. Failure to do so may reduce hunting efficiency and jeopardise their own survival through the winter.

In my study, most Tawny Owls did not breed every third year when vole populations reached the low point in the cycle. In these years many more primary and secondary feathers were moulted, even though food was scarce. Without the constraints of a family, Tawny Owls could spread their

moult over a substantially longer period extending from April/May until September/October. However, even in these years most owls did not undergo a complete moult of primary and secondary feathers.

Virtually all studies of Tawny Owls have shown them dependent on rodents that exhibit pronounced annual population fluctuations (Southern 1970; Delm  e *et al.* 1978; Petty 1987a; Petty 1989). Therefore, annual variations in breeding success related to changes in small mammal abundance are likely to have the same influence on moult. Pieti  inen *et al.* (1984) demonstrated a very similar moult strategy in the Ural Owl *Strix uralensis* in Finland to that of Tawny Owls in Kielder. Most wing feathers were moulted when the birds did not breed or failed in a breeding attempt, and least when three or more chicks were reared. It therefore seems unlikely that other wild Tawny Owl populations would show a substantially different pattern of moult to that described.

Few studies apart from Pieti  inen *et al.* and this study on wing feather moult in owls in the genus *Strix* have been based on recaptures of known individuals in the wild. Some previous accounts have relied heavily on captive birds (e.g. Piechocki 1968). Captive birds are not usually stressed by food shortage or breeding, so they should be expected to moult far more heavily each year compared to wild owls. This may account for the differences in some of the published accounts of wing feather moult in Tawny Owls.

Korpim  ki (1988) studied the moult of primary feathers in wild male Tengmalm's Owl in Finland and found no relationship between the number of feathers moulted and fledglings reared. So the constraint on wing feather moult imposed by reproduction in *Strix* owls may not apply to more mobile owls such as Tengmalm's.

Moult of tail feathers

All accounts of the moult of tail feathers in Tawny Owls suggest that all twelve feathers are moulted annually (Piechocki 1968; Ginn & Melville 1983; Cramp 1985). However, my study shows that most owls moult their tail feathers biennially. All birds of both sexes completely moulted their tail feathers for the first time at their first adult moult in their second year of life (Table 4). Thereafter, in most birds, feathers were replaced every other year. There were at least two instances where owls retained all tail feathers for an extra year. In other cases one or more feathers were moulted out of sequence with the rest (Table 4). The closely-related Spotted Owl *Strix occidentalis* in North America appears to follow a similar biennial tail moult, but the initial replacement of the juvenile tail occurs at the second adult moult in the third year of life (Forsman 1981; Moen *et al.* 1991).

My analysis also shows that tail moult in Tawny Owls was unrelated to the moult of wing feathers, brood size or food supply. The reason why tail feathers appear to have a predetermined moult sequence in contrast to wing feathers may be related to the value of these different feather groups for hunting. Tail feathers are used mainly for steering and braking. These aspects may be far more crucial to a perch hunter like the Tawny Owl than the need for propulsion and lift. Once prey is located, largely by sound, a silent precise descent to the origin of the sound on the ground is vital for successful prey capture.

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