

# WEIGHTS, BREEDING, AND SURVIVAL IN EUROPEAN SPARROWHAWKS

I. NEWTON, M. MARQUISS, AND A. VILLAGE

*Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon PE17 2LS, England*

**ABSTRACT.**—No significant diurnal variation in mean weight was detected in trapped European Sparrowhawks (*Accipiter nisus*). Weights of males fluctuated rather little through the year, but were highest in March and lowest in August. During the breeding cycle, males lost weight slightly in the prelay/early laying periods, when they were feeding females in preparation for egg production, and in the late nestling/postfledging periods, when they were feeding large young. Weights of females fluctuated greatly during the year: they were highest in May at the time of egg laying and lowest in August at the end of breeding. Females increased in weight by 40–50 g (15%) in the 10–20 days before laying; lost about 20 g over the laying period, on average; maintained high weight through much of incubation; and lost weight during the nestling period. The main functions of the extra body reserve are probably to buffer the female against temporary food shortages during incubation and to enable her to feed the chicks preferentially in the nestling period. Females that did not lay eggs remained low in weight throughout the early part of the breeding season and were then significantly lighter than breeders. Moreover, females that laid large clutches were heavier throughout the prelaying and laying periods than were females that laid small clutches, and females that subsequently hatched their eggs started incubation at a significantly greater weight than did those that deserted their eggs. We suggest that clutch size and breeding success are dependent on the female being able to maintain high weight during the periods she is dependent on the male for food and, hence, on the hunting success of the male.

First-year birds of both sexes weighed less than adults throughout the year and were especially light during their first 2 months of independent life. This was probably a period of high mortality, especially in males, in which a clear relationship emerged between weight and survival prospects. Received 27 May 1982, accepted 25 October 1982.

OUR main aim in this paper is to describe the weight changes that occur in European Sparrowhawks (*Accipiter nisus*) through the year, and from one age group to another. Information is also given on wing lengths and on weights in relation to breeding and survival. Previous data on the weights of accipiters are limited, although the breeding season weights of *A. nisus* were discussed by Newton (1979), and the winter weights and body composition of *A. g. gentilis* by Marcström and Kenward (1981). Weights and measurements of migrating *A. g. atricapillis*, *A. striatus*, and *A. cooperii* were given by Mueller et al. (1976, 1979, 1981). Almost all our data were collected in Dumfriesshire, south Scotland, in 1971–1980, during the course of a population study in which birds were trapped for routine marking and identification. More than 1,250 weights were obtained in all. Sparrowhawks were resident in the area throughout the year, and we had no evidence that any passed through on migra-

tion. Most egg-laying occurred in May, so that most young hatched in June, left the nest in July, and became independent of parental care in August. The young dispersed mainly in the first few weeks after becoming independent, and remained relatively sedentary thereafter (Newton and Marquiss 1983).

## METHODS

Birds were caught in live-baited cage-traps placed near nests in the breeding season or on likely hunting areas at other times, but some females were caught in noose traps placed on nests during incubation. When operating cage-traps, we usually drove from one to another throughout the day, checking each trap 2–5 times, depending on the daylight period. We tried to ensure that no hawk was in a trap for more than 3 h before being removed and weighed. When operating noose traps, we remained near the nest and removed each bird within 10 min of capture. Most birds were weighed no more than once in any one year, but about 5% were caught more frequently, and their weights were included more

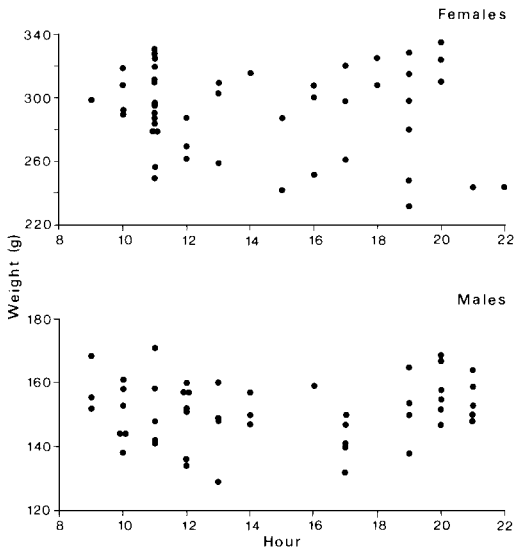


Fig. 1. Weights each hour of the day of juveniles trapped in August. No significant diurnal variation.  $n\sigma = 49$ ,  $n\varnothing = 48$ .

than once if successive captures were more than 5 days apart. Weights were taken to the nearest gram on a Pesola balance, and wing lengths (with feathers flattened and straightened) to the nearest millimeter. In the analysis, details from males and females were kept separate throughout, as were those from juvenile or first-year birds ("brown" plumage, August to next July) and adults ("blue" plumage, all older birds). In any given month, no significant variation in weights was found between years and habitats, so weights for all years and all habitats were pooled throughout. Three main habitats were represented: (1) small woods in mixed farmland on valley floor, and (2) small woods in open grassland grazed by sheep and (3) large conifer plantations in hills.

## RESULTS

*Weights through the day.*—In certain months, enough birds were caught to investigate weight variation during the course of the day. These months included August and September (for juveniles of both sexes), April (for adults of both sexes), and May and June (for adult females only). Diurnal variation was examined from single weighings of different individuals caught at different times of day, rather than from repeat weighings of the same individuals. The weights of juveniles caught in August are given as an example in Fig. 1. In some months, weights seemed to be slightly lower in the

afternoon than in the morning or evening, but in no case was the diurnal variation significant statistically. This was true whether individuals were caught in baited traps or in noose traps on nests. No birds were caught within 2 h after dawn (either in these months or in any other), however, so it is possible that some diurnal variation might have appeared if this time could have been included. Also, less than 2% of trapped birds had food in their crops, and these were mostly hens caught in noose traps. As some birds may have been in cage traps for up to 3 h, they may have lost any crop food before they were examined, but if hunting with a full crop were common, we should have obtained more cases than we did. For the rest of the paper, all weights are combined for particular periods, irrespective of time of day.

*Weights through the year.*—Weights of males fluctuated rather little through the year (Table 1, Fig. 2). The monthly means of adults were at their lowest in August (143 g), near the end of the breeding season, and at their highest in March (155 g), before the start of the next. The monthly means of first-year males varied more than those of adults, but they too were at their lowest in August–September (136–139 g), soon after the first-year birds had become independent of parental care, and at their highest the following March (153 g). In each month, first-year males were lighter than adults, especially in September, November–February, and in June–July, when both groups were feeding young. Over the year as a whole, the average difference in the monthly means of the two age groups was 6.5 g.

Weights of females fluctuated through the year much more than those of males. The monthly means of adults reached their lowest in August–September (258–262 g), around the end of breeding, and became generally higher during November–February. They increased further in March and reached their annual peak in May (325 g), coinciding with egg laying, and then declined again to August (Fig. 2). The weights of first-year females followed a similar pattern, but in all months the means were lower than those of adults, especially in August–September, soon after the first-year females had become independent of parental care, and in March and May (Table 1). Over the year as a whole, the average difference in the monthly means for the two age groups was 14.4 g, or 11.2 g if the obviously unrepresentative De-

TABLE 1. Weights each month through the year of different sex and age groups of *Accipiter nisus* in south Scotland ( $n$  = number,  $m$  = mean, SE = standard error, SD = standard deviation).

Month <sup>a</sup>	Adult males			First-year males <sup>b</sup>			Adult females			First-year females <sup>b</sup>						
	$n$	$m$	SE	SD	$n$	$m$	SE	SD	$n$	$m$	SE	SD				
Aug	9	142.9	4.0	11.9	66	138.6	1.1	8.7	10	262.0	5.0	15.9	29	243.5*	3.9	20.8
Sep	10	149.2	2.9	9.3	53	136.4***	1.2	8.8	15	258.3	3.3	12.7	24	244.7*	5.3	25.2
Oct	3	147.3	2.1	3.6	9	147.0	2.8	8.4	4	262.5	2.2	4.4	5	259.0	11.8	26.4
Nov	8	152.6	2.5	7.0	16	143.6	3.2	12.8	5	279.6	9.3	20.9	4	275.8	12.5	25.0
Dec	4	153.8	3.9	7.8	6	150.8	3.4	8.4	7	277.6	5.9	15.6	1	(228.0) <sup>c</sup>	—	—
Jan	3	152.7	3.0	5.1	6	138.3**	1.9	4.6	10	279.1	9.6	30.2	8	266.8	5.3	14.8
Feb	8	152.0	3.0	8.5	11	143.8	3.6	12.0	9	275.9	5.4	16.1	6	273.7	6.3	15.3
Mar	10	155.1	2.2	7.1	5	152.6	1.9	4.2	7	294.3	7.8	20.5	4	271.0	22.1	44.2
Apr <sup>d</sup>	92	153.3	0.9	9.1	20	150.1	2.0	8.8	92	301.3	2.7	25.7	25	291.5	5.0	25.1
May <sup>d</sup>	70	150.4	1.1	8.9	17	149.8	1.9	7.9	246	324.7	1.7	26.3	43	309.6**	5.0	32.7
Jun <sup>d</sup>	10	153.7	2.3	7.4	2	139.5	11.5	16.3	142	319.0	1.7	20.7	20	308.3*	5.3	23.8
Jul <sup>d</sup>	24	148.8	1.9	9.3	10	143.5	2.7	8.4	55	289.3	2.3	17.4	12	279.4	5.0	17.5

<sup>a</sup> Significance of variation between months: adult males,  $F_{11,238} = 1.77, P > 0.05$ ; first-year males,  $F_{11,208} = 6.83, P < 0.001$ ; adult females,  $F_{11,561} = 32.93, P < 0.001$ ; first-year females,  $F_{11,468} = 17.66, P < 0.001$ .

<sup>b</sup> Significantly different from adults of same sex in same month at 5% level, \*\*1% level, \*\*\*0.1% level.

<sup>c</sup> This bird was very emaciated and seemed about to die from starvation.

<sup>d</sup> Weights for April–July were from birds trapped on nesting territories; birds not associated with such territories were therefore excluded. The existence of such ‘nonterritorial’ birds was known, but we had no reliable estimate of their proportion in the total population.

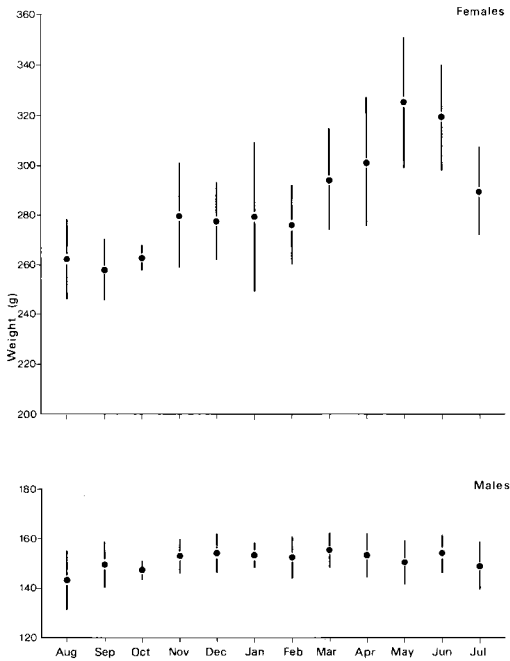


Fig. 2. Mean weights ( $\pm$ SD) of adults each month through the year. Sample sizes and other details in Table 1.

ember weight of first-year females was excluded. Within each sex/age group, the variation through the year was tested by analysis of variance and emerged as highly significant in all groups except adult males, whose weights remained most stable (Table 1). In neither sex was evidence found for age-related weight variation beyond the second year.

*Weights and breeding.*—Weights of adults were also examined in relation to stage of breeding, irrespective the date (Fig. 3). In males, the main features were loss of weight in the prelaying/early laying periods (from about 15 days before the first egg to near clutch completion), a recovery during early incubation, and a marked loss in the late nestling/postfledging periods. In the females, the general trend was for a rapid increase in the 20 days before laying (especially in the 10 days before laying); a peak in the early stages of laying, followed by a loss during the late stages of laying; high weight through much of incubation; and a further loss through the nestling to the postfledging period. Females that were caught on nesting territories in May but that did not lay (some of these territories had new nests and others did

not) showed no weight increase around laying time (Fig. 3). Their weights were then significantly lower than those of females that did lay. On the other hand, nonbreeding males in May weighed as much as breeding males in the same month.

Too few weights were obtained around laying time to draw firm conclusions as to any association there might have been between weight and clutch size, but the findings were suggestive. On average, females that laid 5–7 eggs were heavier in the 5-day period before laying than were other females that laid fewer eggs (Table 2). They were also heavier, on average, in the last stages of laying (6–10 days after the first egg) and in the early stages of incubation. Furthermore, when we compared birds examined in the early and late stages of laying, the weight loss seemed less in birds that laid large clutches than in those that laid small clutches. With one exception, the different means in each row of Table 2 were not significantly different from one another, but regressions of weights on clutch size gave significant relationships for the late laying and early incubation periods, with the heaviest birds associated with the largest clutches (late laying:  $t_{35} = 4.13$ ,  $P < 0.001$ ; early incubation  $t_{97} = 2.19$ ,  $P < 0.05$ ). It thus seemed that large clutches were associated with both a high weight before laying and a relatively small weight reduction during the laying period, whereas small clutches were associated with lower weights before laying and a bigger reduction during laying. At later stages of breeding, in the late incubation and nestling periods, there was no consistent relationship between clutch/brood size and body weights of females.

During the late stage of laying, females that subsequently succeeded in their breeding were significantly heavier than females that failed, the means ( $\pm$ SE) being  $337 \pm 10$  g and  $306 \pm 5$  g, respectively. Only at this stage was such a significant difference found, and most nest failures occurred soon afterwards, as clutches were deserted early in incubation. The ability to maintain high weight through the laying period may therefore have been important for continuing incubation.

*Weights outside the breeding season.*—All birds outside the breeding season were caught in baited traps, so it was of interest to check whether they were likely to have been typical

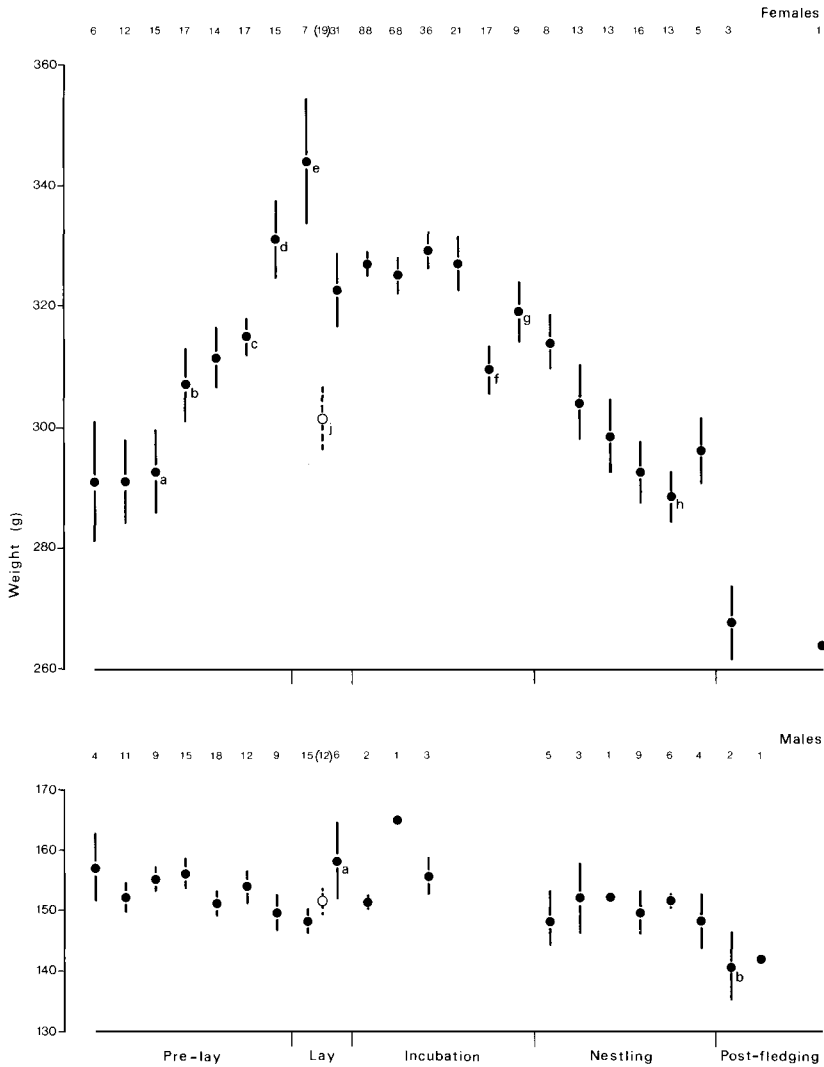


Fig. 3. Mean weights ( $\pm$ SE) of adults each 5-day period through the breeding cycle. Numbers show sample sizes in each period, and open circles refer to nonbreeders. Females above, males below. Mean female weights in the periods labelled a–j were tested and found to differ significantly, as follows: a vs. d,  $t_{28} = 3.85$ ,  $P < 0.001$ ; a vs. e,  $t_{20} = 4.06$ ,  $P < 0.001$ ; b vs. e,  $t_{22} = 3.15$ ,  $P < 0.01$ ; c vs. e,  $t_8 = 2.89$ ,  $P < 0.05$ ; e vs. f,  $t_{22} = 4.05$ ,  $P < 0.001$ ; e vs. h,  $t_{18} = 6.58$ ,  $P < 0.001$ ; f vs. h,  $t_{28} = 3.86$ ,  $P < 0.001$ ; g vs. h,  $t_{20} = 5.02$ ,  $P < 0.001$ ; d vs. j,  $t_{32} = 3.48$ ,  $P < 0.01$ ; e vs. j,  $t_{24} = 4.09$ ,  $P < 0.001$ . Mean male weights did not differ significantly between any two periods, using  $t$ -tests.

of the whole population or underweight (hungry). It was possible to investigate this for juveniles in August–September, when large numbers were trapped. Individuals caught only once were, on average, heavier than individuals caught more than once, but in both sexes the difference was significant only at the 10% level (Table 3). Moreover, those individuals that were caught twice were heavier at their first

capture than at their second capture within these months. This last difference was not significant, even at the 10% level, but appeared in both sexes. While not conclusive, these data gave some grounds for thinking that birds caught in baited traps outside the breeding season may not have been typical (in weight) of the whole population. Any such bias would have been unlikely in the breeding season,

TABLE 2. Weights (g), means  $\pm$  SE (*n*), of female Sparrowhawks at different stages of breeding.

Breeding stage	Clutch size		
	1-3	4	5-7
Prelay (up to 5 days before first egg)	324 $\pm$ 8 (4)	321 $\pm$ 10 (5)	351 $\pm$ 13 (5)
Early laying (up to 5 days after first egg)	333 $\pm$ 5 (4)	318 $\pm$ 10 (3)	351 $\pm$ 15 (4)
Late laying (6-10 days after first egg) <sup>a</sup>	303 $\pm$ 7 (13)*	325 $\pm$ 10 (8)	344 $\pm$ 10 (15)*
Early incubation			
11-15 days after first egg	316 $\pm$ 8 (8)	321 $\pm$ 5 (26)	330 $\pm$ 2 (65)
16-20 days after first egg	310 $\pm$ 8 (6)	321 $\pm$ 6 (20)	328 $\pm$ 4 (43)

<sup>a</sup> Means significantly different:  $t_{26} = 3.30$ ,  $P < 0.01$ .

when birds were caught on their nesting territories, the majority of hens in unbaited noose traps. If anything, the bias at this season may have been toward the heavier birds, for non-breeders and failed breeders were under-represented. This was because, in the later stages of breeding, these last two categories of birds were no longer present on nesting territories, to which trapping at this stage was restricted.

For some months, juveniles were caught in much greater numbers than expected from their proportion in the population, which, to judge from nesting success, never exceeded one per adult. Yet in August, the ratio of juveniles to adults among trapped males was 7.3:1, declining to 0.5:1 in March (Table 4). Among females the equivalent figures were 2.9:1, declining to 0.6:1 in March. (Ratios were even lower in April-July, but in these months birds were caught on nesting territories, which were occupied disproportionately more by adults than by juveniles.) The predominance of juveniles among birds trapped in late summer and autumn may have been due partly to juveniles having more difficulty than adults in getting enough to eat (and hence more readily entering baited traps) and partly to the dispersal of juveniles (which occurred at this time) bringing

a continual stream of fresh individuals into the trapping area. Relatively more juvenile males than juvenile females were caught in late summer, despite an equal sex ratio at fledging (Newton and Marquiss 1979) and despite dispersing males moving around less than females (Newton and Marquiss 1983). The most likely explanation was that juvenile males had greater difficulty in meeting their food needs than did juvenile females, which resulted in a difference in trappability. The sexes took partly different prey species (Newton and Marquiss 1982a), but no marked change in the prey composition of the area occurred in late summer.

For juveniles caught in August-September, we could also examine the proportion that were subsequently recovered in relation to weight at the time of capture (Table 5). Recoveries included some birds trapped alive by ourselves in the study area and others reported dead or dying by other people, either inside or outside the study area. For this analysis, birds known to be alive one month after initial capture are classed as survivors. In both sexes, more of the heavier than of the lighter individuals were subsequently recorded again, but the trend emerged as statistically significant only in males. There was a 10-fold difference in the

TABLE 3. Weights of juveniles in August-September according to frequency and occasion of capture [*n* = number, *m* = mean (g), SE = standard error].

	Males <sup>a</sup>			Females <sup>a</sup>		
	<i>n</i>	<i>m</i>	SE	<i>n</i>	<i>m</i>	SE
Birds caught once	61	138.8*	1.1	33	246.5*	3.9
Birds caught twice						
(a) Both captures	58	135.8*	1.2	20	234.0*	5.0
(b) First capture	29	137.4	1.7	10	241.0	6.9
(c) Second capture	29	134.1	1.8	10	228.2	6.8

<sup>a</sup> \* For males,  $t_{117} = 1.84$ ,  $P < 0.1$ ; for females,  $t_{51} = 1.98$ ,  $P < 0.1$ .

TABLE 4. Number of first-year birds per adult trapped in different months. Based on data in Table 1. Figures for August–March from baited traps placed on hunting areas and for April–July from baited traps placed near nests or from noose traps on nests. The data are comparable within these two periods but not between them (see text).

Month	Males <sup>a</sup>	Females <sup>a</sup>
Aug	7.3	2.9
Sep	5.3	1.6
Oct	3.0	1.3*
Nov	2.0	0.8*
Dec	1.5*	0.1*
Jan	2.0*	0.8
Feb	1.4	0.7
Mar	0.5	0.6
Apr	0.2	0.3
May	0.2	0.2
Jun	0.2	0.1
Jul	0.4	0.2

<sup>a</sup> \* = ratios based on no more than 10 individuals.

proportion recovered between males weighing less than 130 g in these months and those weighing more than 150 g. This presumably meant that the lighter individuals died, a not wholly unexpected event, as the young concerned had only recently left the care of their parents. It was not possible to check survival in relation to weights in other months of the nonbreeding period, because too few birds were caught then.

*Wing lengths.*—In our study areas, male sparrowhawks had wing lengths of 188–211 mm and females of 222–251 mm. There was thus clear separation between the sexes, but roughly similar variation in both. Within each sex, wing length was slightly shorter, on average, in first-year birds than in older ones, but this trait was significant only in females, whose wing lengths increased between year 1 and year 2 and again between year 2 and year 3 (Table 6). No evidence was found for age-related variation beyond age 3, but relatively few birds older than 7 yr were caught. Within 148 pairs, there was no correlation between wing lengths of male and female ( $r = 0.14$ , not significant), indicating no selective mating in this respect. All these wing lengths were from birds captured in the breeding season (April–August), so they should have been comparable with one another in terms of wear. In another respect, however, wing lengths of first-year and older birds may have been less comparable. The individual feather-lengths indicated that first-year birds

TABLE 5. Survival of juveniles in relation to weight in August–October. The data are comparable within sexes but not between them, because the main trapping locality favored males. Based on birds born and trapped in 1971–1977 and known to be alive at least 1 month after trapping. Recoveries include some birds trapped alive by ourselves and others found dead and reported by the public.

	Weight (g) <sup>a</sup>			
	Males	≤130	131–150	≥151
Number caught		19	90	13
Number recovered (%)		1 (5)	26 (29)	7 (54)
	Females	≤220	221–260	≥261
Number caught		7	35	7
Number recovered (%)		0 (0)	7 (20)	3 (43)

<sup>a</sup> Significance of variation among weight classes: males,  $\chi^2 = 9.32$ ,  $P < 0.01$ ; females,  $\chi^2 = 4.04$ ,  $P < 0.2$ .

had more pointed wings than adults and relatively longer, squarer tails (unpubl. information).

Our retrapping in different years showed that the increases in weights and wing lengths with age resulted from changes in individual birds rather than from greater survival of the larger individuals. These trends in *A. nisus* paralleled similar findings on weights and wing and tail lengths in *A. gentilis*, *A. striatus*, and *A. cooperii* (Mueller et al. 1976, 1979, 1981).

## DISCUSSION

The lack of any significant diurnal variation in mean weights presumably resulted from the feeding habits of sparrowhawks, which, for most of the year, take their food in 1–3 large meals each day, separated by long fasts. The weight of an individual may fluctuate greatly during the day, but, as different individuals catch their prey at different times, depending on their hunting success, it was not surprising that the mean weight of the trapped sample showed no marked diurnal trend. The fact that recently fed (high weight) individuals seldom entered baited cage traps added to the impression of stability. During nest watches, too, no diurnal variation was detected in prey deliveries to chicks, either from males or from females (Newton 1978, Geer 1981).

From before the eggs were laid until after they were hatched, the male provided the food for the female and, presumably, influenced her

TABLE 6. Wing lengths of Sparrowhawks of different sex and age ( $n$  = number,  $m$  = mean,  $SD$  = standard deviation,  $SE$  = standard error).<sup>a</sup>

Sex and age (yr)	$n$	$m$	$SD$	$SE$	Range
<b>Males</b>					
1	41	198.95	3.71	0.58	192-209
2	58	200.00	3.68	0.48	193-209
3	18	200.89	4.60	1.08	193-211
All adults (2+)	171	199.52	3.98	0.30	188-211
<b>Females</b>					
1	98	234.10	4.59	0.46	223-246
2	119	235.13	4.58	0.42	224-247
3	43	236.93	5.23	0.80	226-251
All adults (2 +)	476	236.63	4.81	0.22	222-251

<sup>a</sup> Significance of differences: males, 1 vs. 2,  $t_{97} = 1.39$ , ns; 2 vs. 3,  $t_{74} = 0.84$ , ns; 1 vs. 2+,  $t_{210} = 0.83$ , ns; females, 1 vs. 2,  $t_{215} = 1.65$ ,  $P < 0.1$ ; 2 vs. 3,  $t_{160} = 2.13$ ,  $P < 0.05$ , 1 vs. 2+,  $t_{144} = 4.97$ ,  $P < 0.001$ .

weight. The dependence of breeding performance on the weight of the female was suggested by several findings. First, females that laid eggs gained about 40-50 g (15%), on average, in the 10-20 days before laying and became heavier then than at any other time of year. This was due not only to ovarian and egg development but to the accumulation of extra body fat and protein, which was very evident in birds handled at this stage. Individuals that did not put on weight did not lay, though some had built nests, so perhaps high weight was a necessary prelude to laying. Females that did lay lost, on average, only about 20 g in weight over the laying period, but the clutch itself weighed up to 180 g, so egg formation must have occurred chiefly on the strength of food eaten at the time. On three occasions, as part of a different exercise, we removed the male after the female had laid the first egg. In each case no further eggs were laid, although the female remained near the nest and in one case persistently called for food. Such a prompt response could have been due to the shock of losing the male, but it would also be expected if the female were relying day-to-day on food from the male, though not if she were committed to a certain egg number by her initial body condition. Furthermore, the number of eggs laid correlated with body weight. Birds that laid large clutches were heavier in the immediate prelay period than were birds that laid small clutches. A similar difference was even more marked in the late stages of laying and was also evident in early incubation. It was perhaps partly a decline of body condition be-

low a threshold during the laying period that curtailed egg production and resulted in a small clutch.

As weight remained high for much of incubation, one function of the extra body reserve accumulated by females in the prelaying period may have been to provide a reserve to buffer the female against any temporary failure of the male to provide enough food, either during the incubation or early nestling periods. We found from nest watches that prey deliveries by the male were reduced by one-third during rain periods (Newton 1978), so a succession of wet days could have very much reduced the food brought to the female. A body reserve would have enabled the female to continue with incubation over such periods and not to have to desert the clutch to seek her own food. That female weight at the start of incubation was related to the fate of the clutch was indicated by the lower weight in females that subsequently failed than that in those that succeeded. Furthermore, postlaying weights were low in females that produced small clutches, and small clutches were much more often deserted than were large clutches (Newton and Marquiss unpubl.). Presumably males that fed their females insufficiently well in the prelaying period continued their poor performance into incubation, resulting eventually in nest failure because the female had to hunt for herself.

Females that hatched their eggs lost weight throughout the nestling period. This was because, as we learned from nest watches, they gave almost all the food brought by the male



to their young, taking for themselves only the feet and other parts of prey items that the young refused. Thus, another function of the body reserve, if not used during incubation, may have been to enable the females to feed their young preferentially at the expense of their own condition. Small, rapidly growing chicks were more vulnerable to temporary food shortages than their mothers were, so in females that reached this stage of breeding the body reserve seemed even more useful than during incubation. There could have been an advantage in the females losing some weight at this stage anyway, because, from about the time the young were half grown, the females began to help with the hunting and may have flown more efficiently if they weighed less (Freed 1981, Norberg 1981).

The weights of males during the breeding cycle fluctuated less than those of females but showed lows at two crucial times. The first occurred in the prelaying period, coinciding with the time of maximum weight gain in the females. Presumably, the males gave as much food as possible to their females at this stage, even at their own expense, because the clutch size depended on the female's weight. The second low in the males was in the late nestling/postfledging periods, presumably because they, as well as the females, may have fed the young preferentially at this stage.

At no stage did males accumulate such large body reserves as females. This could be attributed to their having to maintain an active hunting role throughout breeding, in contrast to the larger females, which (providing the male could feed them) could adopt a passive storage role for much of the cycle. The advantage of body reserves may have contributed during evolution to the clear division of labor between the sexes and to the female having the storage role. She has to put on some extra weight for egg production anyway and, being larger than the male, has a potentially greater storage capacity. With these conditions, it is a small step to cessation of hunting and to accumulation of even greater reserves to serve during the incubation and nestling periods. The one essential is that the male should be able to supply the food for both. This reasoning would apply to other raptors besides Sparrowhawks.

In examining weights in relation to breeding, we could deal only with associations and correlations, so it was not possible to distin-

guish cause from effect. One interpretation of the data, however, was that female weights were crucial to breeding at all stages: high weight was necessary before the female could begin egg laying, and the maintenance of high weight was crucial to the number of eggs laid and to the continuance of incubation. There is some experimental evidence for this view, in that females that were given extra food in the prelay and laying periods produced earlier and larger clutches than did other females in the same area that were not (Newton and Marquiss 1981). Normally, however, the male supplied the food, so he was ultimately responsible for the condition of the female and thus for the fate of the breeding attempt.

Many small bird species of temperate regions put on extra weight in winter, largely to enable them to survive the long cold nights (King and Farner 1966, Newton 1969). Sparrowhawks, being larger, could presumably withstand short periods of deprivation more readily, and those that we examined showed no sign of a mid-winter peak in weight. They were heavier in November–February than in the preceding months but were heavier still in March, and females were heaviest of all in May–June. The lowest weight recorded for a male was 111 g and for a female 197 g; both were juveniles in August, their weights being about 20% below the average for their age group in this month, and apparently were on the point of starvation. On this basis, and from what is known of the energy needs and tissue composition of raptors (Kirkwood 1981), one can assume that Sparrowhawks at average or above average weight can normally survive a few days without food, females for about half as long again as males. For 2 months after they had first become independent, the young weighed much less than the adults, and, from the results obtained, it seemed that many died from starvation in these months. Hence, the subsequent rise in the mean weight of this age group was probably due partly to the deaths of the low-weight individuals and partly to the improved condition of the remainder. Nonetheless, the weight difference between first-year and older birds was maintained through the rest of the year and disappeared only after the first complete molt.

Ring recoveries had previously indicated that males suffered considerably greater mortality than females in the first year of life, leading to

a surplus of females in the adult population (Newton et al. 1981, 1983). The present results, indicating the predominance of juvenile males in the autumn catches and the clearer relationship between weight and survival in juvenile males than in juvenile females, suggest that this differential mortality occurred largely in the first few months of independent life and was due to more frequent starvation in males. During August–September, juvenile males were much lighter, on average, than during their last few days in the nest in July (136–139 g compared with about 160 g), whereas juvenile females were about the same (258–262 g compared with about 255 g) (nestling weights from Moss 1979), a further indication of greater food-shortage. The males probably also suffered from their smaller body size, which would make them less able than females to withstand any temporary shortages they might experience.

We had little indication that molt influenced weight. Both sexes began molt while breeding, females near their peak weight in May and males in June, and both continued into September or October (Newton and Marquiss 1982b). Both were heavier in the earlier stages than towards the end, but in most individuals molt had been completed for several weeks before mean weight increased again in November. We could not, therefore, readily apply the suggestion of Marcström and Kenward (1981) for Goshawks that low weight during molt was an adaptation to reduce wing loading while flight performance was impaired.

Insofar as they are comparable, the weights of other raptors studied in the breeding season show similar trends to those of Sparrowhawks, and in various owls and Kestrels (*Falco tinnunculus*), female weights are particularly high during the laying and incubation periods (Marples 1942, Hirons 1976, Hardy et al. 1981, Village 1983). As in the Sparrowhawk, the males of these species feed their females from before laying and show much more stable weights for much of the breeding cycle, declining in the late nestling stage. In all these species, therefore, breeding performance may depend upon female body condition, which in turn is dependent upon male hunting success, in the way we have described (following Newton 1979). Similarly, in Tawny Owls (*Strix aluco*), Barn Owls (*Tyto alba*), and Kestrels, as

well as in Sparrowhawks, starvation seemed frequent among juveniles in their first few months of independent life, despite an abundance of food in the environment at that time, perhaps because they were inefficient hunters (Hirons et al. 1979, Hardy et al. 1981, Newton et al. 1982). Furthermore, Goshawk females in winter showed a clear relation between weight and survival prospects, of the type found in Sparrowhawks (Marcström and Kenward 1981). Hence, several of the characteristics of Sparrowhawks may be widespread among other birds of prey.

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