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Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden

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The migration of raptors at Falsterbo, Sweden was studied during five autumns, 1986–1990, to investigate the intraspecific temporal sequence of migration for different age and sex classes. The analysis is based on counts of between 45 and 72 321 individuals of 14 species. The percentage of juveniles varied among species and to some extent between years. This reflects a variable tendency of different migrants to concentrate at Falsterbo and fluctuating breeding success from year to year. Most species showed an even sex ratio. Marked exceptions were Marsh Harrier *Circus aeruginosus* and Hen Harrier *C. cyaneus* in which females constituted 60 and 61% respectively of adult migrants. This biassed sex ratio agrees with the tendency towards polygyny in these species.

In tropical (long-distance) migrants adults migrated ahead of juveniles (Honey Buzzard *Pernis apivorus*, Montagu's Harrier *Circus pygargus*, Osprey *Pandion haliaetus*, and Hobby *Falco subbuteo*). It is suggested that it is advantageous for adults to arrive early on the wintering grounds, finish moult and accumulate energy reserves before spring migration and the next breeding season. Those short-distance migrants in which adults migrated before juveniles at Falsterbo are species whose majority leave Scandinavia in the winter (Hen Harrier, Common Buzzard *Buteo buteo*, Rough-legged Buzzard *B. lagopus*, Merlin *Falco columbarius* and Peregrine *F. peregrinus*). Adults leaving first have a greater possibility to secure a good winter territory forcing the juveniles, migrating later, to settle in less suitable habitat or to winter further south. In species where juveniles migrated ahead of adults a large proportion of the adults spend the winter close to the breeding grounds (Red Kite *Milvus milvus*, Goshawk *Accipiter gentilis* and Sparrowhawk *A. nisus*). The presumably subdominant juveniles may be excluded from the breeding territories by the adults and therefore migrate south, followed by a varying proportion of adults.

Females generally migrated before males at Falsterbo due to different moult strategies; females starting and finishing moult of the flight feathers before males. This difference in timing of moult and migration is ultimately dependent on a marked role division between the sexes during the breeding cycle. In Honey Buzzard where both sexes share the breeding duties equally no difference in timing of migration was found. Social dominance, importance of early arrival at the winter quarters and moult strategies are the factors best explaining the observed differential timing in migrating raptors at Falsterbo.

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Introduction

Intraspecific variation in migratory birds with respect to seasonal timing of migration and distribution during the non-breeding season has been referred to as differential migration (Gauthreaux 1978, Ketterson and Nolan 1983). Variation may occur between populations, sex

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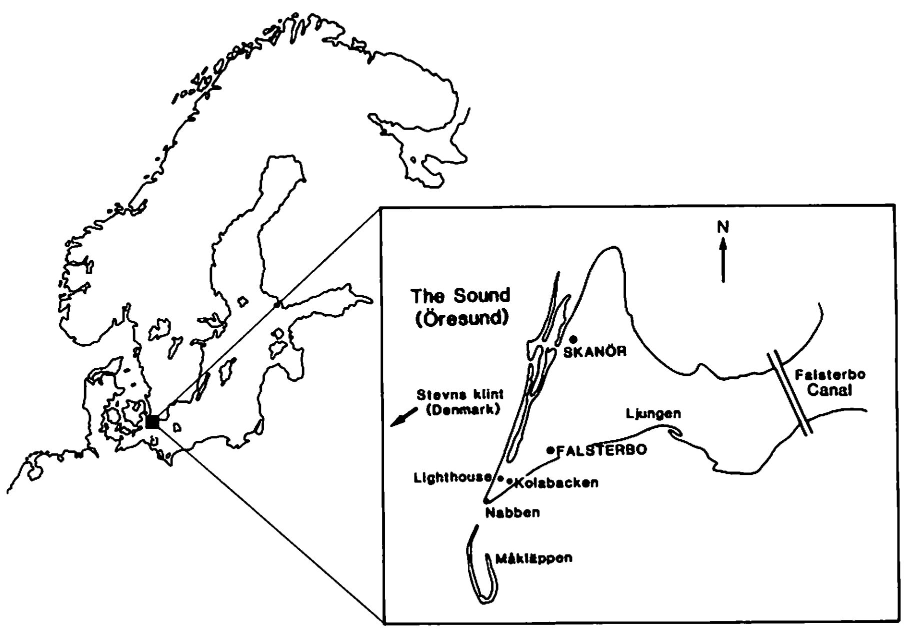
Fig. 1. The study area on the Falsterbo peninsula, Sweden.



and age classes and individuals. Differential migration by age and sex classes of migrant raptors is summarized in Kerlinger (1989). Published data on seasonal differences in the timing of autumn migration are heterogeneous and somewhat contradictory. This study describes the temporal sequence of autumn migration shown by sexes and age groups of a large number of raptor species passing Falsterbo in South Sweden.

The Falsterbo peninsula constitutes the southwesternmost point of Scandinavia (Fig. 1). Large numbers of migrants, especially those reluctant to cross large bodies of open water, are concentrated here during autumn migration making Falsterbo one of the best places in Europe to observe raptor migration. Counts of passing birds of prey were begun in the 1940s (Rudebeck 1950). Later, a ten-year study covering the period 1949–1960 was published (Ulfstrand et al. 1974). Since 1973 standardised counts of migrants have been carried out by the National Environmental Protection Board from 11 August until 20 November (Roos 1991 and earlier).

With the development of better binoculars and the use of telescopes it has become possible to scrutinize migrant raptors more closely. The publication of field guides such as Christensen et al. (1974), Forsman (1984) and Gensböl (1984) has made it possible to determine their age and sometimes sex.

In autumn 1986 I estimated the percentage of juveniles among migrating Honey Buzzards and Red Kites (scientific names given below) at Falsterbo as a part of conservation projects on these species. In connection with this all raptors were counted and in many cases aged and sexed. I continued these studies during 1987–1990, covering the entire autumn migration of birds of prey from the beginning of August until mid-November. The ambition was to distinguish juveniles from adult birds and when possible to sex the migrants.

Study area and methods

Migrating raptors pass over the Falsterbo peninsula in a westerly to southwesterly direction towards Denmark (Fig. 1). To age and sex as many individuals as possible, my co-observers and I chose observation sites as close to the main migration stream as possible. Because of diurnal changes in the spatial pattern of migration counts were normally started on the southwesternmost point, Nabben, in the morning. Later we often moved to other sites to see the migration better. The places most often used were the Lighthouse, Kolabacken, Ljungen and the Falsterbo Canal (Fig. 1). An advantage of selecting a counting site further to the east was that the birds were usually at a lower elevation there. If wind conditions changed during the day it was sometimes necessary to change observation post to get closer to the passing raptors.

The characters used in separating age and sex were generally those given by Forsman (1984). We attained almost complete coverage from 1 August until 20 November each year. On days with bad weather, such as storm and rain, when migration is practically nonexistent, the counts were normally cancelled. Observations started at dawn and continued as long as any migrating raptors were seen. This normally means sometime in

Table 1. Total number of raptors of different categories at Falsterbo in the autumns of 1986–1990. Subadults are included in adults.

	Adults			Juveniles			Sex or age		Total
	♂	♀	Σ	♂	♀	Σ	♀/juv	unident.	
Honey Buzzard *Pernis apivorus*	3098	2942	24257			3801		862	28922
Black Kite *Milvus migrans*			26			8		4	38
Red Kite *M. milvus*			243			1291		264	1798
White-tailed Eagle *Haliaeetus albicilla*			17			11		5	33
Griffon Vulture *Gyps fulvus*			1						1
Short-toed Eagle *Circaetus gallicus*			4						4
Marsh Harrier *Circus aeruginosus*	216	273	489			1594	356		2439
Hen Harrier *C. cyaneus*	206	198	404			418	469		1291
Pallid Harrier *C. macrourus*	3		3			2			5
Montagu's Harrier *C. pygargus*	13	6	19			24	2		45
Goshawk *Accipiter gentilis*	3		3	30	18	133		2	138
Sparrowhawk *A. nisus*	832	740	1572	1534	1419	2953		67796	72321
Common Buzzard *Buteo buteo*			10189			6305		39958	56452
Long-legged Buzzard *B. rufinus*						1			1
Rough-legged Buzzard *B. lagopus*	321	258	2914			959		1728	5601
Lesser Spotted Eagle *Aquila pomarina*			31						31
Spotted Eagle *A. clanga*			3						3
Steppe Eagle *A. (rapax) nipalensis*			2			2			4
Imperial Eagle *A. heliaca*			1						1
Golden Eagle *A. chrysaetos*			4			4		1	9
Booted Eagle *Hieraaetus pennatus*			2						2
Osprey *Pandion haliaetus*			222			214		570	1006
Eurasian Kestrel *Falco tinnunculus*	111	109	297			684		1285	2266
Red-footed Falcon *F. vespertinus*	2		2			4			6
Merlin *F. columbarius*	24	6	32			88	365	620	1105
Hobby *F. subbuteo*			12			96		108	216
Gyr Falcon *F. rusticolus*						4			4
Peregrine *F. peregrinus*	21	15	49	12	10	38		19	106

the afternoon, but on some days migratory movements continue almost until dusk. On days with many birds at least two observers worked together, usually the author and A. Jönsson. Other skilled raptor-counters contributed on single days during the five years. Observers used binoculars 10×40 and wide-angle telescopes 30×70. It is impossible to observe all birds of prey passing the peninsula. Although the majority pass in a "corridor" right above the observation point, small numbers of Sparrowhawks, harriers and falcons migrate low along the horizons. Wind conditions sometimes displace the raptors to the north or south of the Falsterbo peninsula, making identification of age and sex difficult.

One problem is to decide how many of the raptors turn back. This problem increases the further eastwards on the peninsula the count is made. Generally fewer migrants turn back if the weather conditions for migration are good. Some species are more hesitant to cross the sea than others. All birds seen returning or judged to have spent the night on the peninsula were subtracted from the totals. It was not always possible to register all returning migrants as some birds turn far out over the sea, later to return inland north of the peninsula. In Honey Buzzard, Sparrowhawk, harriers, Osprey and falcons this normally was no problem because they usually hesitate little before crossing. The most difficult species in this respect is the Common Buzzard. At the end of August mainly young Common Buzzards often circle over the central peninsula without migrating, and even in September-October the rate of returning birds can be close to 100% on single days. On those problematic days the counts were most often made at the Lighthouse, where it was easier to register return movements. A check of the daily totals is possible through comparison with counts made at Stevns Klint on the opposite side of the strait, where the raptors departing from Falsterbo reach Danish land after a successful sea crossing. Most often the daily counts there are slightly lower but in accordance with those at Falsterbo, but under certain wind conditions higher figures are sometimes obtained at Stevns Klint (Tim Andersen in litt.). On some days with easterly winds most raptors seen at Falsterbo constitute "drop-outs" that come in from the sea after leaving land north of the peninsula. Altogether the counts reflect raptor passage over the Falsterbo peninsula with varying coverage for different species.

The differences in seasonal timing (the median date (Md), i.e. when 50% have migrated) between age and sex categories have been tested statistically with a Kolmogorov-Smirnov two-sample test (with sample sizes equal to the number of identified individuals, Siegel 1956). The results are given under each species below.

Table 2. Total number of individuals counted and the proportion of juveniles of different raptors at Falsterbo in 1986–1990.

	1986	% juv	1987	% juv	1988	% juv	1989	% juv	1990	% juv	1986 –1990	% juv
Honey Buzzard	6858	37	3959	6	6954	4	7357	9	3794	7	28922	14
Red Kite	291	84	243	75	313	89	499	83	452	86	1798	84
Marsh Harrier	261	74	281	74	444	74	729	79	724	81	2439	78
Hen Harrier	342	65	150	75	180	62	356	55	263	40	1291	59
Montagu's Harrier	3	0	4	50	6	67	13	54	19	58	45	58
Goshawk	30	100	31	100	15	93	19	89	43	100	138	98
Sparrowhawk	15712	–	14722	79	11379	78	16069	77	14439	83	72321	78
Common Buzzard	7094	31	10770	36	11914	51	13264	37	13410	36	56452	38
Rough-l. Buzzard	1367	27	1480	34	852	29	955	28	947	6	5601	25
Osprey	159	–	102	26	251	38	255	56	239	66	1006	50
Eurasian Kestrel	374	70	478	68	388	73	606	68	420	70	2266	70
Merlin	272	–	242	88	228	87	158	83	205	93	1105	90
Hobby	71	94	29	100	36	89	48	83	32	81	216	87
Peregrine	28	42	15	29	20	35	28	64	15	33	106	46

Results

The total number of each age- and sex class during the five years is given in Table 1 for all raptor species observed. Thirteen species, occurring in less than 40 individuals in the period, were excluded from the analysis. The proportion of undetermined birds (with respect to age and sex) varies from only 1% in Goshawk and 3% in Honey Buzzard to 94% in Sparrowhawk. In some species, for example Hen Harrier, a large proportion is

Table 3. Median date of different sex and age categories of raptors at Falsterbo in 1986–1990. In certain years when the sexes were not separated, the median is given under male.

	1986	1987	1988	1989	1990	1986–90
Honey Buzzard, ad	30 Aug	30 Aug	28 Aug	26 Aug	24 Aug	27 Aug
Honey Buzzard, juv	12 Sep	17 Sep	5 Sep	9 Sep	13 Sep	11 Sep
Red Kite, ad	24 Sep	29 Sep	2 Oct	29 Sep	17 Oct	30 Sep
Red Kite, juv	24 Sep	29 Sep	2 Oct	24 Sep	27 Sep	26 Sep
Marsh Harrier, ♂	9 Sep	15 Sep	5 Sep	26 Aug	28 Aug	1 Sep
Marsh Harrier, ♀	9 Sep	31 Aug	27 Aug	27 Aug	26 Aug	28 Aug
Marsh Harrier, juv	8 Sep	1 Sep	30 Aug	27 Aug	26 Aug	26 Aug
Hen Harrier, ♂	20 Sep	27 Oct	30 Sep	8 Sep	26 Aug	13 Sep
Hen Harrier, ♀	18 Sep	17 Sep	15 Sep	27 Aug	26 Aug	3 Sep
Hen Harrier, juv	24 Sep	29 Sep	2 Oct	29 Sep	8 Oct	1 Oct
Goshawk, juv ♂	1 Nov	26 Oct	30 Oct	31 Oct	4 Nov	2 Nov
Goshawk, juv ♀					22 Oct	25 Oct
Sparrowhawk, ad ♂		17 Oct	19 Oct	24 Oct	16 Oct	22 Oct
Sparrowhawk, ad ♀		13 Oct	3 Oct	23 Oct	16 Oct	19 Oct
Sparrowhawk, juv ♂		21 Sep	1 Oct	25 Sep	1 Oct	25 Sep
Sparrowhawk, juv ♀		16 Sep	7 Sep	6 Sep	2 Sep	9 Sep
Common Buzzard, ad	18 Sep	29 Sep	11 Oct	27 Sep	27 Sep	30 Sep
Common Buzzard, juv	5 Oct	17 Oct	11 Oct	30 Sep	17 Oct	11 Oct
Rough-legged Buzzard, ♂	25 Sep	17 Oct	11 Oct	5 Oct	12 Oct	5 Oct
Rough-legged Buzzard, ♀				29 Sep	8 Oct	2 Oct
Rough-legged Buzzard, juv	4 Oct	18 Oct	11 Oct	30 Sep	17 Oct	8 Oct
Osprey, ad		25 Aug	28 Aug	22 Aug	24 Aug	26 Aug
Osprey, juv		1 Sep	30 Aug	27 Aug	27 Aug	29 Aug
Eurasian Kestrel, ♂		17 Sep	8 Sep	3 Sep	29 Aug	12 Sep
Eurasian Kestrel, ♀					25 Aug	1 Sep
Eurasian Kestrel, juv		17 Sep	5 Sep	4 Sep	28 Aug	8 Sep
Merlin, ♂		10 Oct	22 Sep	8 Sep	8 Sep	6 Oct
Merlin, ♀						31 Aug
Merlin, juv	18 Sep	20 Sep	22 Sep	18 Sep	29 Sep	21 Sep
Hobby, ad	2 Sep	–	24 Aug	27 Aug	25 Aug	27 Aug
Hobby, juv	15 Sep	19 Sep	7 Sep	8 Sep	29 Aug	10 Sep
Peregrine, ad	15 Sep	14 Sep	31 Aug	3 Sep	2 Sep	9 Sep
Peregrine, juv	17 Sep	28 Sep	21 Sep	20 Sep	1 Oct	22 Sep

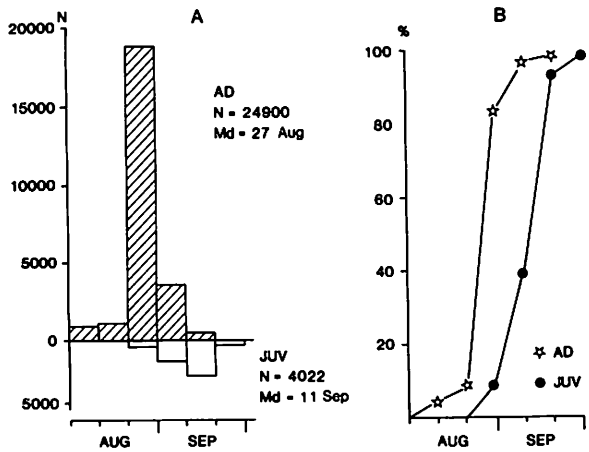


Fig. 2. Honey Buzzard. The total material from 1986–1990 is used and separated into ten-day periods. 2A shows a histogram with adults (second-year birds or older) above and juveniles below the x-axis. The sexes were separated in all species in which this is possible. Total number of individuals counted (N) and median date (Md), i.e. when 50% have migrated, are given for each category. 2B is a cumulative graph showing the percentage of each category having migrated at a certain time. This graph better visualizes differences in timing between sex and age categories.

labelled "♀/juv" meaning that they were either adult females or juveniles. In most species the proportion of unidentified birds decreased over the five years as the observers' experience increased.

The overall seasonal timing and total proportions of different sex and age classes were estimated for each species on the basis of the samples of identified individuals (with respect to sex and age), weighted by the total number of individuals during ten-day periods. For example, if 20% of the identified Common Buzzards in the last ten-day period of September during the five years were juveniles, 20% of the unidentified Common Buzzards in this period were also assumed to be juveniles and the rest adults. In the same way the group ♀/juv was divided between females and juveniles according to their proportions among the identified individuals for each ten-day period. Detailed information on the proportion of identified birds in different ten-day periods is given below for the different species.

In the presentation below, generally one histogram is given for each species showing the seasonal distribution of adults (second year birds and older) above the x-axis and juveniles below it. When possible, sexes have been separated. The median date (Md) is given for each category together with the total number of individuals counted (N). The sample sizes of identified individuals, with respect to age and sex classes, are given in Table 1. Furthermore, a cumulative graph shows the total percentage of various categories having migrated at a certain time. This graph also demonstrates differences in seasonal timing between age and sex categories.

The variation in numbers between single years was considerable for some species. Table 2 shows annual totals and percentages of young birds together with the five-year average. Median dates in different years are compared with the overall five-year median date in Table 3 for the most numerous and regular migrants.

Honey Buzzard *Pernis apivorus*

The Honey Buzzard is the dominant raptor in August. Adults normally begin to migrate in the middle of August, show a pronounced peak in the last week of the same month, after which the migration quickly wanes (Fig. 2). In 1988 nearly 900 birds migrated in the first ten days of August, probably a result of a collapse of the main food supply, wasps (Tjernberg 1989). The number of adult Honey Buzzards varied between 3500 and 6700 in the five years, and this variation is presumably governed mainly by weather factors, as suggested by Ulfstrand (1958).

The juveniles culminate two weeks after the adults (Table 3) and odd birds are seen into October. The difference in median date between young and older Honey Buzzards is highly significant ($p < 0.001$).

In 1988–1990 a number of adult birds were sexed (Table 1). The estimated proportion of males (calculated from the proportion of sexed individuals weighted by the total number of individuals in different ten-day periods) was 51%, indicating an even sex ratio. Contrary to most other species in which the sexes can be distinquished, there seems to be no difference in migration time between male and female Honey Buzzards.

Compared with other raptors the proportion of juvenile Honey Buzzards at Falsterbo is low, on average 14% (Table 2). Only occasional second year birds are recorded at Falsterbo, supporting the view that they normally spend their first summer in the wintering areas in Africa.

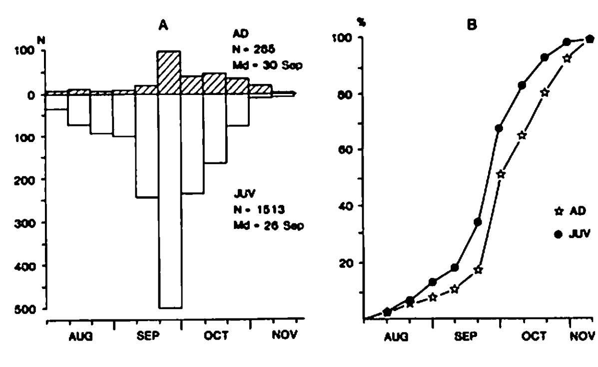


Fig. 3. Red Kite. Explanation is given under Fig. 2.

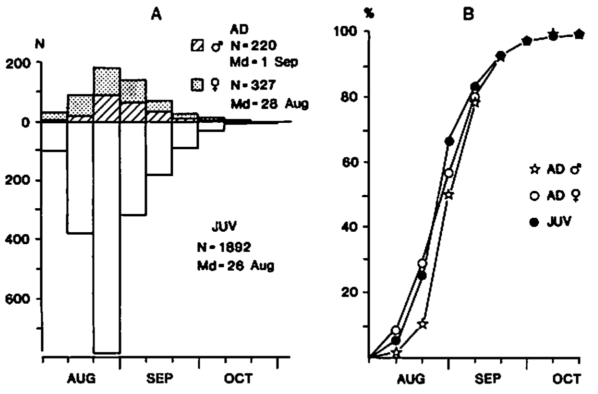


Fig. 4. Marsh Harrier. Explanation is given under Fig. 2.

Red Kite *Milvus milvus*

After a marked decrease in the first half of the 20th century the number of Red Kites has been increasing steadily in Sweden since 1970 (Risberg 1990) and the breeding population is now about 300–400 pairs, mostly in the southernmost part (P.-O. Andersson pers. comm.).

The migration season is very protracted (Fig. 3). After moderate numbers of primarily young birds in August, numbers rise to a maximum in late September. In a few years large numbers were recorded well into October. The Red Kite is dependent on thermals and the migration often occurs on a few peak days with up to 100 migrating birds.

The proportion of juveniles was very high in all years (Table 2), with an overall average of 84%. After having been strongly migratory the Red Kite started wintering in Sweden around 1960 (Ulfstrand 1963). The majority of adult kites are nowadays resident and spend the winter in southernmost Sweden. Studies of the age composition of wintering kites have revealed between 10 and 12% juveniles (Kjellén 1990). It is possible that many of the migrating "adults" are immature birds.

In the first three years there was no difference in median date between adults and juveniles (Table 3). With greater numbers in October in 1989 and 1990 the adults culminated markedly later. The difference in the whole five-year material is only four days, but highly significant ($p < 0.001$).

Marsh Harrier *Circus aeruginosus*

The migration increases in the middle of August and culminates in the last ten days of this month (Fig. 4). Numbers decrease all through September and few birds linger into October. Harriers migrate on a broad front and the concentration at Falsterbo is less marked than for other species (Rudebeck 1950). The data revealed 13% adult females, 9% adult males and 78% juveniles. With an average production around 2 fledged young per breeding pair (Newton 1979, Cramp et al. 1980), juveniles are overrepresented . Adults may be less inclined to follow leading-lines during migration. The proportion of juveniles varied little over the five years (Table 2). The average median dates fell in the order juveniles, adult females and adult males (Table 3). The difference in timing between young birds and females ($p < 0.05$) as well as that between females and males ($p < 0.001$) is significant.

Among the adult Marsh Harriers females outnumbered males. The proportion of males varied between 33 and 48% in the five years, with an average of 40%. Because the sexes have different migration periods, the weather during their respective peak period may affect the annual proportions. However, it is likely that the sex ratio among adult birds is in fact biassed in favour of females. This is interesting in the light of the rather high tendency towards polygyny in this species (Newton 1979, Cramp et al. 1980).

A total of 48 (22%) of the males were in their second year, indicating that a large portion of these sexually immature birds return to the breeding grounds. The median date of these younger males (30 Aug) is one day earlier than that of older males.

Hen Harrier *Circus cyaneus*

In Scandinavia the Hen Harrier is primarily a bird of the northern coniferous zone. A few spend the winter in southern Sweden but the vast majority migrate south as far as the Mediterranean region. Males are easily distinguished, while a large portion was classified as ♀/juv (Table 1). The migration season covers most of the autumn (Fig. 5). In August adults, with a majority of females, dominate completely. The August figures are higher in certain years, which may reflect poor breeding success. The number of adults then slowly decreases until November. The juveniles do not start migrating until the beginning of September. The peak falls in late September or early October, depending on weather conditions.

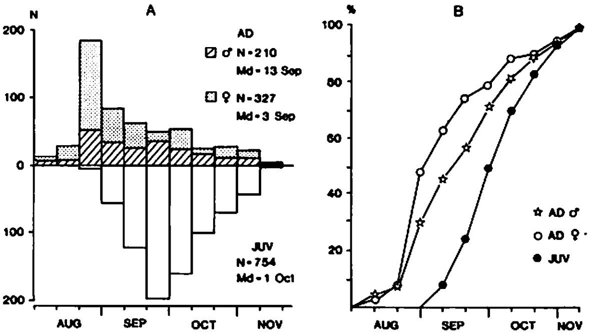


Fig. 5. Hen Harrier. Explanation is given under Fig. 2.

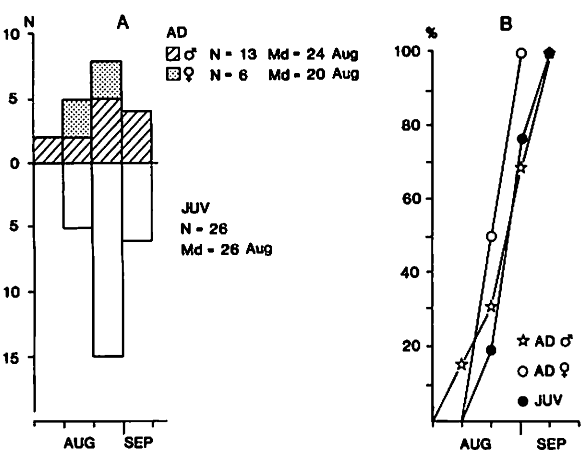


Fig. 6. Montagu's Harrier. Explanation is given under Fig. 2.

The production of young is dependent on rodent numbers in northern Scandinavia (Watson 1977, Alerstam 1990). Even if the study period did not include any pronounced peak year for rodents, the proportion of juveniles varied much more than in Marsh Harrier (Table 2). This variation is in accordance with the other northern rodent specialist, the Rough-legged Buzzard.

As in Marsh Harrier females on average migrated before males, but in contrast juveniles were later than adults in the Hen Harrier (Table 3). The differences in median date are significant between females and males ($p < 0.01$) as well as between males and juveniles ($p < 0.001$). In agreement with these results, Haugh (1972) recorded females before males, but there is conflicting information about the sequence of age groups; Palmer et al. (1988) reported that juveniles migrate first in North America.

As in Marsh Harrier there was a majority of females among the adult Hen Harriers (61%), with some variation between years. A distorted sex-ratio in favour of females has been reported from the Orkney Islands (Balfour and Cadbury 1979) and polygyny is even more frequent than in the Marsh Harrier (Newton 1979).

A total of six second-year males were identified, comprising only 3% of the total number of adult males. These had a six days earlier median date (9 Sep) than the other older males. Second-year males are much harder to distinguish than in Marsh Harrier so this category is most certainly underrepresented.

Montagu's Harrier *Circus pygargus*

Montagu's Harrier is a tropical migrant with a migration peak in late August (Fig. 6). The median dates fall in the order females, males and juveniles, but the differences are not significant. However, they seem representative, with females before males as in most other species and adults ahead of juveniles as in other tropical migrants such as Honey Buzzard, Osprey and Hobby.

Of the 13 recorded males as many as seven (54%) were second-year birds. This contradicts the assumption that most Montagu's Harriers spend their first summer on the wintering grounds in Africa (Cramp et al. 1980).

Goshawk *Accipiter gentilis*

The Goshawk is a common breeder in Scandinavia, most birds being more or less resident. Only small numbers reach Falsterbo (Table 1). The passage was very late with a peak in late October-early November (Fig. 7).

Most Goshawks were aged (Table 1). Of these, only three were adults, and all were males and they passed late in comparison with the median date for juveniles. In the last two years of the study a number of young Goshawks were sexed on the basis of size. It was estimated that 61% of the juveniles were males. As in the Sparrowhawk, young females culminated earlier than young males. The differences in median date between different categories in Goshawk fit well into the general pattern and most likely reflect the true situation; however, due to small sample sizes they are not statistically significant.

Sparrowhawk *Accipiter nisus*

The Sparrowhawk was the most numerous migrant in all five years with a total of over 70000 birds (Table 2). In favourable conditions it is possible to determine the sex in both adult and juvenile Sparrowhawks, which was

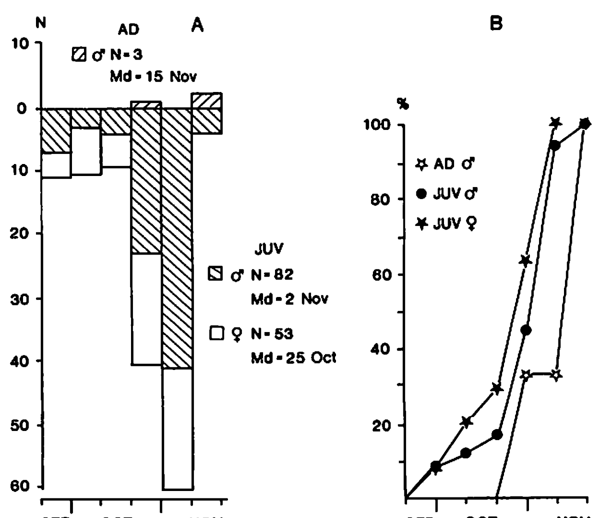


Fig. 7. Goshawk. Explanation is given under Fig. 2.

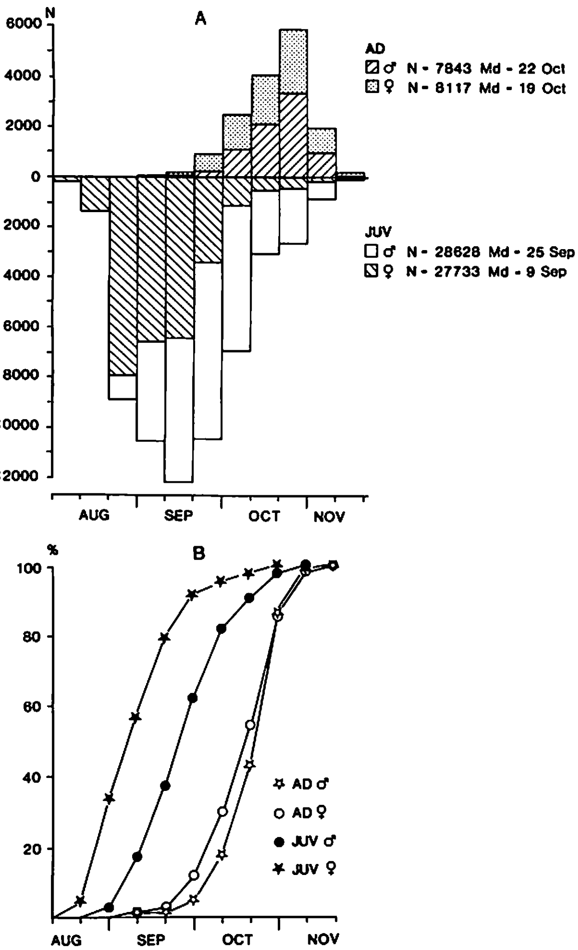


Fig. 8. Sparrowhawk. Explanation is given under Fig. 2.

done for a subsample of birds from 1987 onwards. The migration is often on a broad front and at different altitudes. Since adult males can be distinguished at a longer range, only birds closer than 100 m from the observer and low enough to allow a view of the upperside, were included in the identified sample. Under these conditions all Sparrowhawks can be aged and sexed, yielding an unbiased sample. All identifications were done from the southwesternmost point, Nabben, where the birds generally pass relatively low. All Sparrowhawks migrating at higher elevations were classified as unidentified even though it was possible to age and sex a few of them.

Sparrowhawks migrated throughout the entire period (Fig. 8). Young females predominated in August, but small numbers migrated into November. Juvenile males increased through September and numbers did not decline until November. Adults were scarce before late September, and did not peak until mid-October, with females earlier than males. The median dates fell in the order juvenile females, juvenile males, adult females and adult males (Table 3). The separation was only three days between the adult females and males but all differences were highly significant ($p < 0.001$). The same sequence of migration has been recorded among Sparrowhawks ringed at Falsterbo Bird Observatory (Göran Walinder pers. comm.) and in the closely related Sharp-shinned Hawk *Accipiter striatus* in North America (Rosenfield and Evans 1980).

The Sparrowhawk has increased again after a decline in the 1960s (Risberg 1990) The proportion of juveniles was high during the five-year period (Table 2), indicating successful breeding. Adults presumably predominate in the population that winters in southern Sweden.

The proportion of males among the juveniles varied between 40 and 58% in different years. This variation may be caused by yearly differences in weather during the main periods of passage for the two sexes. The average of 51% in the whole material indicates an even sex ratio. This is exactly the same percentage as Newton (1986) recorded in a large number of broods from Great Britain. Also among the adult Sparrowhawks the proportion of males varied between years with an average of 49% in the whole material.

Common Buzzard *Buteo buteo*

With between 7000 and 13 000 individuals counted annually (Table 1) the Common Buzzard was the second-most numerous raptor. It is to a great extent dependent on thermal soaring migration and the main passage is generally concentrated to a few peak days. Juveniles predominated in late August (Fig. 9). Numbers increased in September when adults were in a clear majority. The temporary decline in early October most likely was an effect of less suitable weather for migration during this study, but the bimodal seasonal pattern could reflect the passage of different populations. The proportion of juveniles was significantly higher in the last 10 days of October, while numbers in November were small.

Mainly dependent on the weather, median date varied rather much over the five years (Table 3). In most

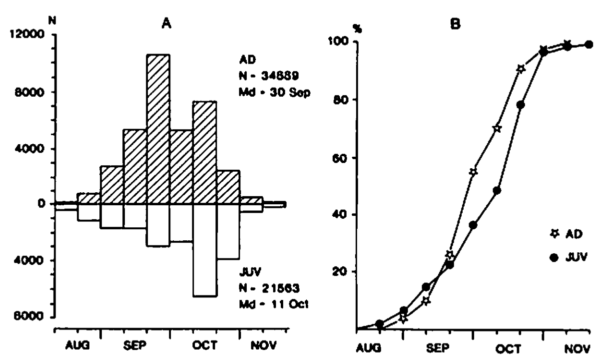


Fig. 9. Common Buzzard. Explanation is given under Fig. 2.

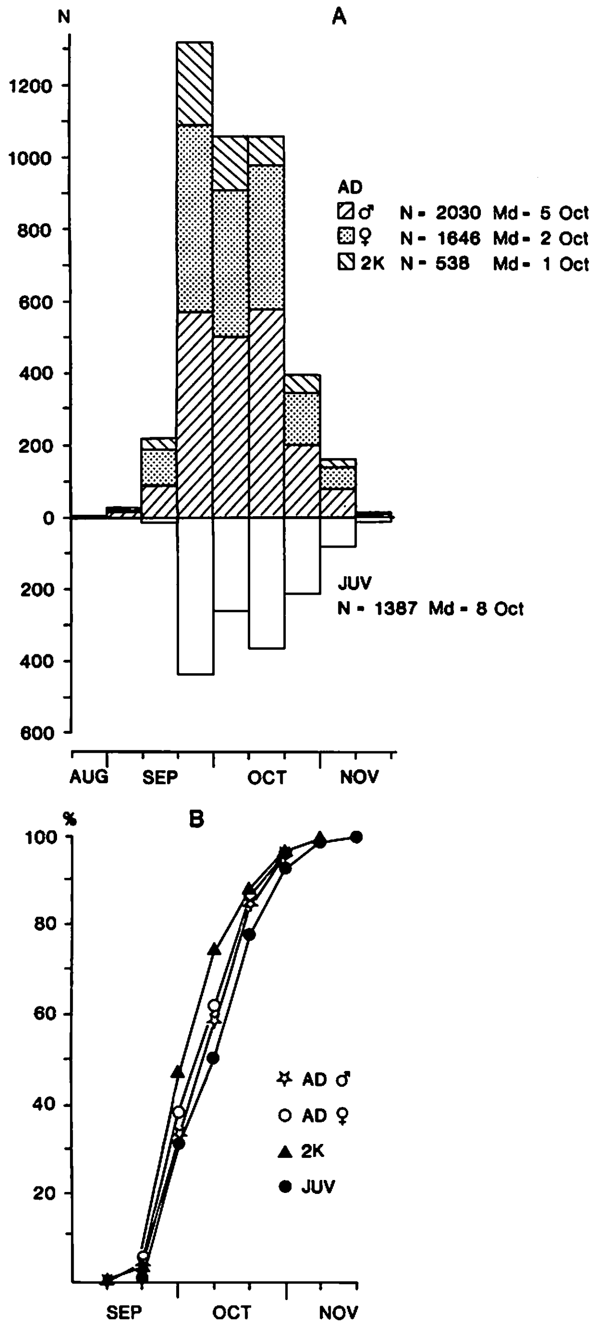


Fig. 10. Rough-legged Buzzard. Explanation is given under Fig. 2. Second-year birds (2K) have been separated from older adults.

years juveniles culminated later than adults. The overall median dates for adults and juveniles are eleven days apart ($p < 0.001$). Broekhuysen and Siegfried (1970) demonstrated an earlier arrival of adults of the subspecies *B. b. vulpinus* (Steppe Buzzard) on the South African wintering grounds.

The proportion of juveniles varied between 31 and 51%, with an average of 38% (Table 2). The highest value, recorded in 1988, probably reflects a good breeding result in that year, but the question is how well the numbers counted at Falsterbo reflect breeding success. A number of immature non-breeders were most certainly included in the figures for adults, but on the other hand the proportion of adults is much higher among Common Buzzards wintering in southern Sweden (Kjellén 1990). If adults and juveniles are assumed to be equally concentrated at Falsterbo, 38% young birds points to an average production of slightly above one young per breeding pair. This is in accordance with values from northern Europe (Newton 1979, Cramp et al. 1980).

Rough-legged Buzzard *Buteo lagopus*

The Rough-legged Buzzard breeds in northern Scandinavia and most birds migrate to Central and Eastern Europe in winter (Risberg 1990, Dobler et al. 1991). In contrast to other raptors it is often more numerous on the Swedish east coast than at Falsterbo. It does not hesitate as much as Common Buzzard to cross open water. The passage is often fast and concentrated to a few peak days. In 1986–90 these peaks occurred from the last days in September until mid-October (Fig. 10).

The majority of birds were aged, and in 1989–1990 adults were separated in adult males, adult females and second-year birds when possible (Table 1). In four of the five years juveniles culminated later than adults (Table 3). The overall median date for adults (3 Oct) was five days earlier than the median date for juveniles ($p < 0.001$). Adults culminated in the order second-year birds (1 Oct), adult females (2 Oct) and adult males (5 Oct); these differences are not statistically significant, but fit the general pattern well. The sex ratio among adults was somewhat unequal with 55% males.

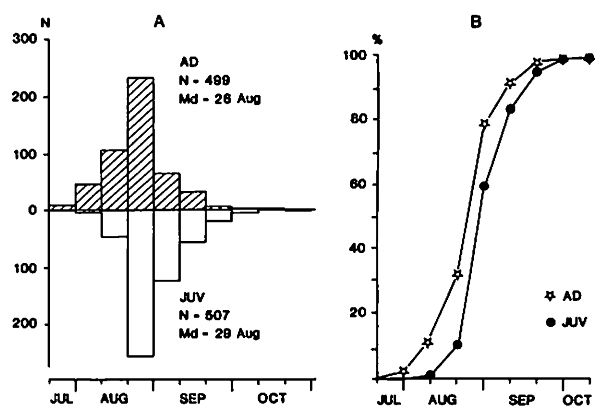


Fig. 11. Osprey. Explanation is given under Fig. 2.

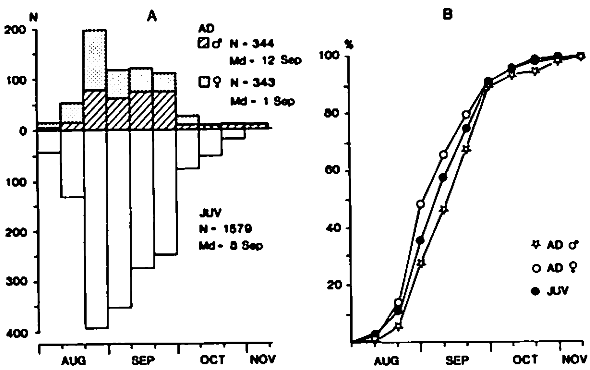


Fig. 12. Eurasian Kestrel. Explanation is given under Fig. 2.

Osprey *Pandion haliaetus*

The Osprey has a breeding population of 3200 pairs in Sweden (Risberg 1990). To a considerable extent Ospreys migrate by flapping flight rather than thermal soaring and so do not become especially concentrated at Falsterbo, with only a thousand birds counted in the five years (Table 2). Adults and juveniles have been distinguished since 1987, resulting in a total proportion of 43% identified (Table 1). Numbers increased reaching a marked peak in late August, after which they declined rapidly (Fig. 11).

As in other tropical migrants, adults migrated before juveniles in all years ($p < 0.001$, Table 3). Earlier migration of adults has also been demonstrated on the basis of ringing recoveries (Österlöf 1977). The proportion of young birds varied between 26 and 66% (Table 2). In 1990 a total of 35 adult Ospreys were sexed. These data suggested an earlier median date for females (24 Aug) than males (27 Aug). The difference is not significant but fits the general picture.

Eurasian Kestrel *Falco tinnunculus*

The Kestrel is the most common falcon in most of Scandinavia, with highest breeding densities in the north. Small numbers spend the winter in southern Sweden but the majority migrates further south. Males, females and juveniles were distinguished. A total of 43% of the migrants in the five years were aged and sexed (Table 1). The main migration period lasted from August until the end of September, but small numbers passed during the whole study period (Fig. 12). Males had a less pronounced peak than the other two categories.

In single years the differences in timing between various categories were small. Overall order of median dates are females, juveniles and males (Table 3), the only significant difference being between females and males ($p < 0.05$), with no clear separation between the two age classes.

The proportion of males among the identified adults varied a great deal between years. In the whole material the sex ratio was equal with 50% males. Since males are easier to identify it is possible that they are slightly overrepresented among the few identified adults in the first years, but this should not seriously affect the whole material. Adult males dominate among Eurasian Kestrels wintering in southern Sweden (Kjellén 1990).

Merlin *Falco columbarius*

The Merlin is a bird of the northern mountains. The majority migrate to western Europe and very few winter in Scandinavia. It is not hesitant to cross open water and thus is not concentrated at Falsterbo. Migration is often on a broad front, resulting in a high proportion of unidentified birds (56%). Since females and juveniles are difficult to separate, a large proportion (33%) was labelled ♀/juv (Table 1). Although few adults were seen there is no reason to believe that the identified sample does not give a representative picture of the seasonal pattern of migration.

Juveniles showed a pronounced migration peak in late September, while females culminated before and males after this date (Fig. 13, Table 3), resulting in median dates in the order females, juveniles and males. Males and females combined had a median eight days before the juveniles. The difference between the sexes is significant ($p < 0.01$) as well as that between adults and juveniles ($p < 0.05$). In eastern North America females peak two weeks before males (Clark 1985).

The proportion of juveniles was high in all years (Table 2), indicating that adults are less concentrated at Falsterbo during migration. Only 10% adults is a very low proportion . The weighted total proportion of males among the adults was 52%.

Hobby *Falco subbuteo*

The Hobby is a tropical migrant with an estimated Swedish breeding population of 1000 pairs (Risberg

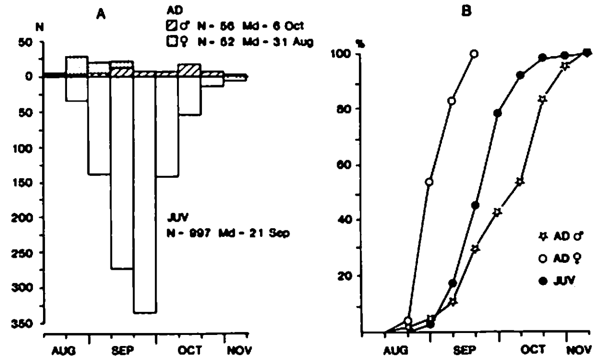


Fig. 13. Merlin. Explanation is given under Fig. 2.

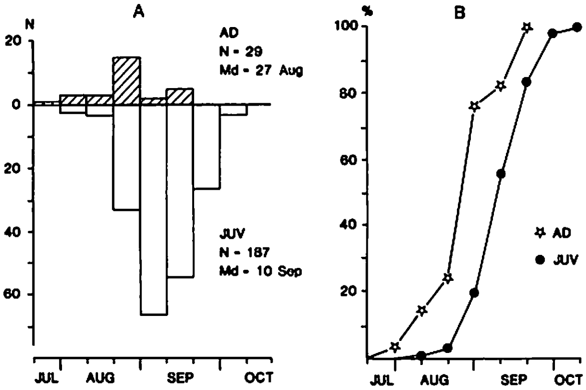


Fig. 14. Hobby. Explanation is given under Fig. 2.

1990). The concentration at Falsterbo is low with annual totals between 29 and 71 individuals (Table 2). Half of the migrants could be separated into adults and juveniles (Table 1). Like Merlin juvenile Hobbies are obviously more concentrated than adults at Falsterbo, comprising 87% of the total (Table 2). The few adults culminate in late August, while young birds peak in the first half of September (Fig. 14). The significant difference in median date ($p < 0.01$) was 14 days, a pattern similar to that in other tropical migrants.

Peregrine *Falco peregrinus*

After a marked population decline since the turn of the century the Peregrine is now slowly recovering in Scandinavia (Risberg 1990). The species shows a leapfrog migration pattern (Cramp et al. 1980) and the few birds wintering in southern Sweden probably originate from this region. A few individuals showing characters of the subspecies *F. p. calidus* seen at Falsterbo indicate that some migrants may come from far northeast.

With only 106 birds in the five years, the Peregrine is a rare migrant at Falsterbo. Most birds were aged and some were sexed (Table 1). The migration season lasted from late August until mid October with a peak in the first half of September (Fig. 15). Adults culminated well before juveniles and the difference in median date is significant ($p < 0.01$). The same order was recorded in Texas by Hunt et al. (1975), who also found the migration of adults to be faster than that of juveniles.

The proportion of young birds varied rather much between years (Table 2). This could be caused by the small material and/or less suitable weather for migration during the peak of either age category. An average proportion of 54% adults is considerably higher than in the smaller falcons (Table 2). With an average production of slightly above one young per breeding pair (Newton 1979, Cramp et al. 1980), juveniles were still overrepresented at Falsterbo, but the bias was not as extreme as in Merlin and Hobby.

Among the sexed birds in Table 1, adult males showed an earlier median date than adult females by 3 days and juvenile males preceded juvenile females by on average 10 days. This is in marked contrast to all other species were the sexes can be separated. The material is small and the differences not statistically significant. However, Hunt et al. (1975) describe studies from Texas where young males precede young females in autumn.

Discussion

There are two reasons for observed differences in timing of migration between ages and sexes. Either they start migration at different times or the migration speed is dissimilar. These factors may work together to increase or cancel differences in timing between categories. Information on the time of departure from the breeding territories by different sex and age categories of raptors is sparse. Adults would seem capable of faster movements due to more experience in catching prey and in navigation. Adult Peregrines migrate faster than juveniles in North America (Hunt et al. 1975). It seems reasonable that the differences in timing demonstrated by the counts at Falsterbo arise as a consequence of both dissimilar speeds and times of departure.

Newton (1979) states that adults remain on their breeding areas each year as long as food permits. Species dependent on cold-blooded prey are resident for a shorter time because of a more restricted period of prey availability. Changing prey numbers in different years can also lead to a varying proportion of the population wintering on the breeding grounds. Because various ages and sexes may be dependent on different prey and are more or less skilled at finding and catching prey, this may affect the timing of departure.

Information on differential migration by age and sex classes in raptors has been compiled by Kerlinger (1989). These data had been acquired from migration counts, banding studies during migration and studies on

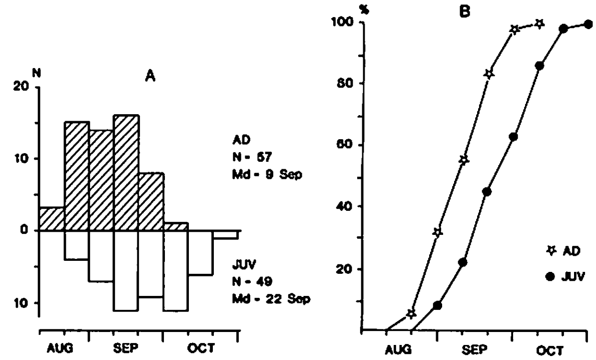


Fig. 15. Peregrine. Explanation is given under Fig. 2.

Table 4. Differences in timing between ages and sexes of raptors on autumn migration at Falsterbo. (s) = statistically significant difference.

Ages	Sexes
Adults migrate before juveniles	*Females migrate before males*
Honey Buzzard (s)	Marsh Harrier (s)
Hen Harrier (s)	Hen Harrier (s)
Montagu's Harrier	Montagu's Harrier
Common Buzzard (s)	Juvenile Goshawk
Rough-legged Buzzard (s)	Adult Sparrowhawk (s)
Osprey (s)	Juvenile Sparrowhawk (s)
Merlin (s)	Rough-legged Buzzard
Hobby (s)	Osprey
Peregrine (s)	Eurasian Kestrel (s)
	Merlin (s)
No difference between adults and juveniles	*No difference between sexes*
Eurasian Kestrel	Honey Buzzard
Juveniles migrate before adults	*Males migrate before females*
Red Kite (s)	Adult Peregrine
Marsh Harrier (s)	Juvenile Peregrine
Goshawk	
Sparrowhawk (s)	

the breeding grounds. The material is heterogeneous and the results in some cases contradictory. Kerlinger concludes that there is no predominant trend in whether adults precede juveniles or vice versa. Table 4 summarizes differences in timing of migration between age and sex classes at Falsterbo.

Differences between ages

Newton (1979) suggested that in long-distance migrants adults precede juveniles while it is the other way round in short-distance (most often partial) migrants. The results from Falsterbo show that in tropical migrants, whose entire populations winter south of the Sahara, adults migrate before juveniles. These include Honey Buzzard, Montagu's Harrier, Osprey and Hobby. Other data (Schifferli 1967, Newton 1979) suggest that the Black Kite also belongs to this group. All these species have an arrested moult started on the breeding grounds and completed in the winter quarters (Cramp et al. 1980). Adults often show obvious signs of moult when migrating at Falsterbo. The adults may depart first because they are able to reach migration body condition faster (Newton 1979). Generally older birds migrate faster and during a more narrowly defined time interval. They normally leave before food is becoming scarce. This may be advantageous in two ways. First, if adults leave there is more food left for their inexperienced juveniles to accumulate energy reserves before migrating. Second, fast migration suggests that it is of great importance to reach the wintering grounds early. Early arrival may be associated with a greater chance of securing a good winter territory. This favours the successful and rapid completion of moult and accumulation of energy reserves before the spring migration and the next breeding season. That food conditions on the wintering grounds in Africa are crucial for the breeding success in the following spring has been demonstrated for the White Stork *Ciconia ciconia* (Dallinga and Schoenmakers 1984). Even for resident Common Buzzards in southern Sweden it has been suggested that the adult birds are constrained to complete breeding and moult in time to be able to survive the poor food conditions of the coming winter (Sylvén 1982). Earlier migration at Falsterbo in years of poor breeding success, as indicated for the Honey Buzzard and Hen Harrier, may reflect an urge to reach the winter quarters early (but may also reflect a sparser food supply on the breeding grounds).

Even among short-distance migrants adults often migrate before juveniles at Falsterbo, suggesting that Newton's (1979) grouping is too general. These species include Hen Harrier, Common Buzzard, Rough-legged Buzzard, Merlin and Peregrine. Small numbers of all five species winter in southern Scandinavia, but the majority migrate to continental Europe. The main advantage of the earlier migration of adults may, as in tropical migrants, be a better chance to secure a good winter territory. As a result the less dominant juveniles, migrating later, settle in less suitable habitat or are forced to migrate further south.

Those short-distance migrants in which juveniles migrate before adults at Falsterbo (Red Kite, Goshawk and Sparrowhawk) are species in which a large part of the adult population winters close to the breeding grounds in Scandinavia. In all three species juveniles have been shown to winter farther south than adults (Schelde 1960, Haukioja and Haukioja 1970, Mueller et al. 1977, Kjellén 1990). Also in Snowy Owl *Nyctea scandiaca* in North America juveniles winter south of adults (Kerlinger and Lein 1986). Young birds may be driven away from the breeding territories by their parents or are less able than adults to cope with the reduced winter prey availability at northerly latitudes. Therefore they migrate south followed by a varying proportion of adults. Newton (1979) suggests that food shortage can act both as an ultimate and proximate factor in influencing whether any particular individual will depart on migration or not. Common Buzzard and Peregrine (Kerlinger 1989), and probably other partial migrants as well, show a leapfrog migration pattern, where northerly populations migrate past more southerly ones and winter furthest to the south. Also British (Mead 1973) and Swedish (Wallin et al. 1985) populations of Eurasian Kestrel show leapfrog migration.

The Marsh Harrier, a species wintering in the Mediterranean region and Africa (Cramp et al. 1980) stands out as an exception, since juveniles migrate before adults at Falsterbo. The differences between males, females and juveniles have varied between single years and are only a few days in the whole material (Table 3). I can think of no good reason why this species deviates from the general rule that in migratory tropical raptors adults migrate before juveniles. Possibly the adults require time to accumulate energy reserves before migration. However, they do not normally complete moult before leaving, since many migrants at Falsterbo show distinct traces of moult of remiges and rectrices.

Differences between sexes

Females migrate before males in most species (Table 4). The sexes often have distinct roles in the breeding cycle (Newton 1979, Cramp et al. 1980). Normally the female incubates and stays close to the nest when the young are small, while the male does the hunting. This has led to a difference in moult strategy and timing which explains much of the differences in migration schedule between the sexes at Falsterbo. Information on moult for the different species is given by Cramp et al. (1980) and Forsman (1984). Normally the female starts moulting during incubation in April–May, when she loses her first remiges. The male, bringing food for the female, is more dependent on intact flight feathers. He normally starts moulting remiges 2–6 weeks after the female. An earlier start of moult in females has been recorded in all species in which females culminate before males on migration at Falsterbo, except Osprey (Table 4). In some cases males perform a faster and more concentrated moult at the end of the breeding season, but normally females still complete their moult before males.

Short-distance migrants normally complete the moult before departing on autumn migration. In the Sparrowhawk, females in Britain commence moult in May, one month ahead of the males. Both sexes can arrest moult for more than a month during the breeding. The complete moult cycle takes 110–130 days in females and 100–120 days in males, and is finished in September–October (Newton and Marquiss 1982). In tropical migrants the moult is arrested during the autumn migration. Thus in Montagu's Harrier the females usually change 6–7 and the males 3–4 primaries before moving south (Forsman 1984). In the Osprey the moult is continuous with two to three moult waves occurring in the wing at the same time (Prevost 1983).

Usually the immatures start their first complete moult in the spring of their second year, slightly earlier than the breeding females. As a consequence, the immature birds normally complete their moult ahead of older birds. If the onset of autumn migration is governed by the timing of moult (birds do not depart on migration until moult is completed), immatures should be expected to migrate before adults. Second-year birds have only been separated in a few species at Falsterbo. Although data are limited, the results support the above argument. In both Marsh and Hen Harriers second-year males culminate on migration before older males, and in Rough-legged Buzzard immatures peak slightly before adults. The few adult Lesser Spotted Eagles *Aquila pomarina* also showed a later median date compared with subadults. Results from the ringing at Falsterbo Bird Observatory show an earlier migration of second-year than adult Sparrowhawks (Göran Walinder pers. comm.).

The Honey Buzzard showed no separation in timing between the sexes. In this species the male takes part in incubation, and both sexes seem to start moult simultaneously at the end of July. Normally they shed only 2–3 primaries and some individuals have not started moult at all before they fly south (Forsman 1984). This probably explains why there is no marked differential migration among adult Honey Buzzards.

In only one species, the Peregrine, did males culminate before females at Falsterbo. The material is rather small and differences not significant, but the pattern was found in both adults and juveniles. An earlier passage of young males than young females has also been observed in Texas (Hunt et al. 1975). Females begin to moult first as in most other species and there seems to be no difference in moult strategy compared with other raptors. Since females are claimed to winter further north than males (Cramp et al. 1980), it is possible that the markedly smaller males are less able to compete on the breeding grounds and thus leave earlier.

Another observation that cannot be explained by moult strategies is the earlier migration of young females as compared with young males in Goshawk and Sparrowhawk. Even though more young male Goshawks migrate, young females peak earlier at Falsterbo. This may indicate that the larger sized and presumably dominant females migrating first fill up suitable winter territories forcing males to extend their migration further south. Competition is the likely cause of the more northerly wintering range of both adult and young female Goshawks as compared with the males (Haukioja and Haukioja 1970, Mueller et al. 1977). Belopolskij (1971) found female Sparrowhawks from German ringings to winter north of males, while Saurola (1981) did not record any such difference on the basis of Finnish recoveries. An earlier migration by young female Sparrowhawks, as observed at Falsterbo, may be advantageous in securing a winter territory as far north as possible.

Explanations of differential migration

Kerlinger (1989) describes six hypotheses that have been invoked to explain why males and females or adults and juveniles migrate at different times and/or to different winter ranges. They all assume that there are costs associated with migrating too far, not far enough, too soon, or too late. Of the six, the Arrival Time Hypothesis and the Character Divergence Hypothesis can only explain differences in winter ranges and are not discussed further, while the other four are commented on below.

The Social Dominance Hypothesis (Gauthreaux 1978, 1982, Mueller et al. 1977, Newton 1979) proposes that differences in seasonal timing of migration and winter distribution of partial migrants are related to social status. Less experienced birds (juveniles) and the smaller sex (in raptors normally males) are supposed to migrate further from the breeding grounds and on an earlier autumn migration schedule than adults and females respectively. This pattern has been demonstrated in passerines. Most data on winter distribution of raptors support the idea of adults wintering north of younger birds (Newton 1979, Kerlinger 1989). The timing of autumn migration at Falsterbo clearly shows that juveniles do not always migrate ahead of adults in short-distance migrants. This, however, does not necessarily mean that they do not winter further south (see discussion above). I believe that social dominance can explain some of the observed differential migration in partially migrating raptors, especially the differences in winter distributions but less of the differences in timing of migration.

The Body Size Hypothesis (often referred to as Bergmann's rule) predicts that larger individuals should winter further north since they are better able to tolerate cold temperatures and can fast longer than smaller individuals. Thus in raptors in which females generally are larger than males, the former are expected to winter furthest to the north. This seems to be true in some species with a marked sexual dimorphism (Newton 1979, Kerlinger 1989, Kjellén 1990). In falcons, however, males sometimes winter north of females (Gauthreaux 1985). From this theory males can be expected to leave first in autumn, which is clearly not the case at Falsterbo (Table 4). Also juveniles ought to leave first which is often not the case.

Rosenfield and Evans (1980) and Duncan (1982) proposed a Feeding Efficiency Hypothesis. Juvenile Sharp-shinned Hawks were assumed to migrate ahead of adults because they are less efficient at capturing avian prey, and therefore it is important for them to migrate in some synchrony with the masses of migrating passerines. This might be true in some cases but the hypothesis does not explain why young females generally leave before young males in Sharp-shinned Hawk in North America and Sparrowhawk at Falsterbo. Table 4 also shows that adults often migrate ahead of juveniles in long-distance as well as in short-distance migrants.

The Moult Hypothesis was suggested to explain the differential timing of migration in American Kestrel *Falco sparverius* (Smallwood 1988) as a need to complete moult before migration. It has also been suggested to explain differences in timing of the autumn migration related to age, sex and population (Kerlinger 1989). Different moult strategies seem to govern the marked difference in migration pattern between Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea* (Alerstam 1985). This hypothesis best explains the observed differences in timing at Falsterbo. Female raptors migrate before males since they commence and finish moult earlier. In those short-distance migrants in which juveniles migrate before adults completion of the moult may be an important reason why adults delay migration. In long-distance migrants and in the Peregrine, the moult of older birds is arrested during autumn migration and finished in the winter quarters. Thus, adults of these species can fly south ahead of juveniles. Obviously, the tropical winter quarters offer, in contrast to temperate winter grounds, living conditions which are favourable enough to allow the birds to moult after arrival at their winter destination. There are however four short-distance migrants in which adults on average leave before juveniles at Falsterbo: Hen Harrier, Common Buzzard, Rough-legged Buzzard and Merlin. According to the literature (Cramp et al. 1980, Forsman 1984) all four finish the moult in September-October before migration. However, adults of these species often show distinct signs of flight feather moult when migrating at Falsterbo, especially early in autumn (August-September). It seems that the urge to migrate south is greater than the need to complete the moult. Possibly also these species sometimes arrest the moult for a shorter period during peak migration.

The above hypotheses are not independent of each other and a combination of different factors is likely to affect the differential migration in raptors. A Migration Threshold Hypothesis, combining aspects of several other hypotheses was presented by Baker (1978). This mathematical approach was criticised by Ketterson and Nolan (1983) for lacking predictive power.

To summarize, in my view social dominance, importance of early arrival at the winter quarters and moult are the factors best explaining the observed differential timing among sexes and ages in migrating raptors at Falsterbo.

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