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Annual variation in numbers, age and sex ratios among migrating raptors at Falsterbo, Sweden from 1986–1995

Nils Kjellén

Department of Animal Ecology, Ecology Building, S-223 62 Lund, Sweden

Summary

The annual variation in age and sex ratio among raptors passing the Falsterbo peninsula, Sweden was studied the ten autumns 1986–1995. The analysis encompasses thirteen species with average annual totals of between 25 and 14,000 migrants. In general, raptors occurring in low numbers showed the greatest relative annual variation. One explanation for high variation was the steep increase in the Swedish populations of Red Kite *Milvus milvus* and Marsh Harrier *Circus aeruginosus* during the period. A constant high percentage of juveniles may be due to the adults being primarily residents, like in Red Kite and Goshawk *Accipiter gentilis*, or to a less pronounced tendency of adults to follow leading lines, as in Marsh Harrier, Merlin *Falco columbarius* and Hobby *F. subbuteo*. In most other species the ages were represented in more balanced proportions, and the proportion of juveniles most likely reflects variations in breeding results. An average of 41% juveniles in Common Buzzard *Buteo buteo* compared to 23% in the Rough-legged Buzzard *B. lagopus* indicates a considerably better production in the first species during the ten years. The extremely low average of 11% young Honey Buzzards *Pernis apivorus* most likely represents a very low production in the period. There was a highly significant correlation in the annual proportion of juveniles between Northern Harrier *Circus cyaneus* and Rough-legged Buzzard. Most likely this covariation reflects fluctuation in rodent numbers in northern Scandinavia. Most species showed a sex ratio close to 50%. In both Northern and Marsh Harrier there was however a clear dominance of females among the adults, with a ratio of 1.63 and 1.27 females/male respectively.

Key words: birds of prey, differential migration, migration counts, breeding success, population fluctuations

Zusammenfassung

Jährliche Zahlen und Alters- und Geschlechtsanteile ziehender Greifvögel in Falsterbo, Schweden, von 1986 bis 1995

Die jährliche Variation der Alters- und Geschlechterverhältnisses bei Greifvögeln, die die Halbinsel Falsterbo in Südschweden überfliegen, wurde im Herbst 1986–1995 untersucht. Die Untersuchung umfaßt dreizehn Arten mit jährlich durchschnittlich 25 bis 14.000 ziehenden Vögeln. Die weniger häufigen Arten waren in ihrem jährlichen Auftreten variabler als die häufigen Arten. Ursache dafür ist die starke Zunahme in der schwedischen Population des Rotmilans und der Rohrweihe in dieser Periode. Einen konstant hohen Anteil an Jungvögeln zeigten Arten, bei denen die Altvögel vorwiegend Standvögel sind (z. B. Rotmilan, Habicht) oder Arten, bei denen die Altvögel weniger intensiv Leitlinien folgen, wie Rohrweihe, Merlin und Baumfalke. Bei den meisten anderen Arten waren die Altersklassen mehr ausgeglichen. Bei ihnen spiegelt der jährliche Anteil an Jungvögeln wohl vornehmlich die Brutergebnisse wider. Durchschnittlich 41% Jungvögel beim Mäusebussard verdeutlichen einen besseren Bruterfolg als 23% Jungvogelanteil beim Rauhfußbussard. Mit durchschnittlich nur 11% Jungvögel war der Bruterfolg des Wespenbussards sehr niedrig, und die jährlichen Anzahlen junger Wespenbussarde variierten sehr stark. Zwischen Kornweihe und Rauhfußbussard korrelierten die jährlichen Jungvogelanteile eng. Dies deutet auf Fluktuationen der Kleinsäuger in Nordskandinavien hin, die beide Arten in gleicher Weise beeinflussen. Ähnliches gilt wohl auch für den Merlin. Die Geschlechterverhältnisse waren bei den meisten Arten ausgeglichen. Bei Kornweihe und Rohrweihe überwogen die Weibchen, mit 1,63 bzw. 1,27 Weibchen pro ziehendem Männchen. Dies dürfte die Folge der bei diesen Arten ausgeprägteren Polygynie sein. Beim Habicht überwogen junge Männchen.

Introduction

Studies of migrating raptors have traditionally only separated different species (e.g. Porter & Willis 1968, Evans & Lathbury 1973). At Falsterbo, the southwesternmost point of Scandinavia (Fig. 1), the autumn migration has been studied since the early 1940s (Rudebeck 1950, Ulfstrand et al. 1974). The development of better binoculars, especially telescopes, and of more advanced field guides has however made it possible to determine the age as well as the sex in many species. This enables a much more profound evaluation of the annual figures. In autumn 1986 I started a more detailed study of the raptors passing the peninsula, trying to separate ages and sexes as far as possible. Earlier the differential timing between sex and age groups during the first five years have been analysed and published (Kjellén 1992). This study accounts for the annual variation in age and sex ratio among raptors passing Falsterbo during the ten-year period 1986–1995. The annual number of migrants varied between 27,000 and 40,000 and this is the first time such a comprehensive data set is presented. It answers questions like: How many of the migrants are juveniles in the different species and how much does this proportion vary annually? Is the variation synchronised between species? How does the sex ratio vary among the migrants? I then discuss the underlying causes of the differences found in various raptors. Important factors causing variation between years may be: 1. A general increase or decrease in the population during the period, 2. Variation in the proportion spending the winter north of Falsterbo, 3. Different concentration rates to Falsterbo in single years due to more or less favourable weather during the peak migration of a certain category and 4. Variation in the breeding result due to changing prey densities.

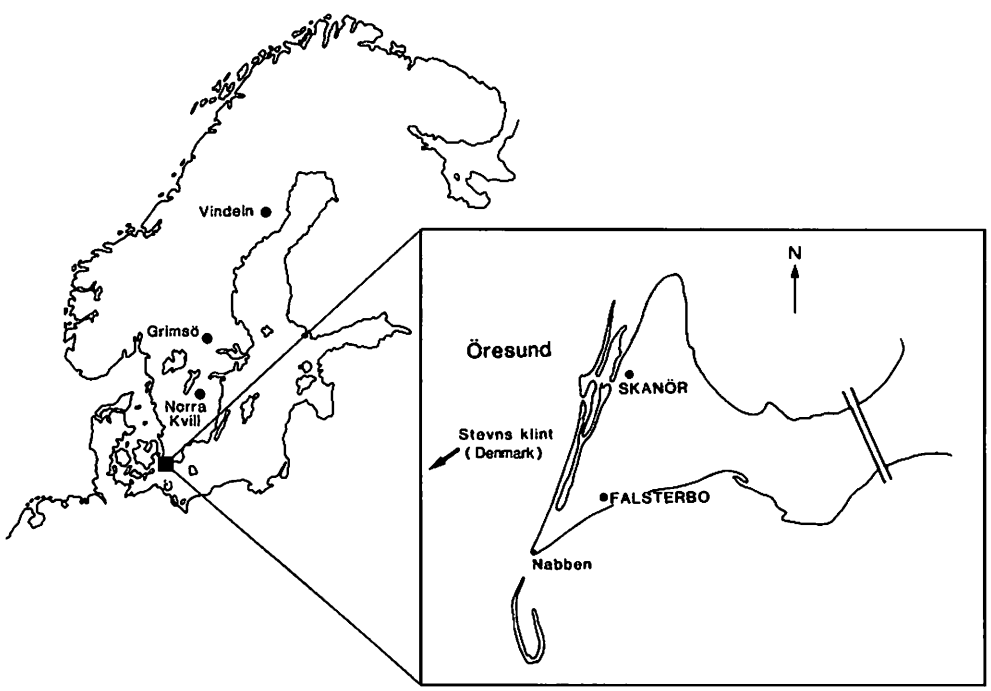

Fig. 1. The study area on the Falsterbo Peninsula and the position of the vole trapping sites in Sweden.
Abb. 1. Das Untersuchungsgebiet auf der Halbinsel Falsterbo und die Lage der Fanggebiete der Kleinnager in Schweden.

Methods

During the ten years 1986–1995 the raptor migration over the Falsterbo peninsula was counted during the period from 1 August until 20 November. Observations started at dawn and continued as long as any significant migration was observed (normally some time in the afternoon). On days with bad weather, such as storm and rain, when migration is practically nonexistent, the counts were often cancelled. During the first years there were a few species where ages and sexes were not separated, but subsequently all birds were aged and sexed as far as possible using characters described by Forsman (1984) and Génsbøl (1995). Migrating raptors pass over the peninsula in a westerly to southwesterly direction towards Denmark (Fig. 1). Dependent on the prevailing wind conditions, different observation points on the peninsula were chosen to be as close to the main migration stream as possible. Most observations were performed by the author but several other observers relieved on single days. On days with many birds at least two observers were normally working together. We used binoculars 10 × 40 and wide-angle telescopes 30 × 70. The ambition was to count as many as possible of the raptors passing Falsterbo. Although the majority often pass in a 'corridor' right above the observation point, it is impossible to cover all individuals in species like harriers and falcons, migrating on a broader front (cf. Kjellén 1992 for a more detailed discussion on the coverage).

The proportion of unidentified birds, with respect to age and sex, varied from only 1% in Goshawk and 8% in Honey Buzzard to 92% in Eurasian Sparrowhawk (Table 1). In the great majority of species over half of the migrants were identified. Although only 8% of the sparrowhawks were aged and sexed, this sample still contained around a thousand individuals annually. Since adult male sparrowhawks 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 upper side, were included in the identified sample. Under these conditions all sparrowhawks can be aged and sexed, yielding an unbiased sample. In most raptors juveniles are not harder to identify at a distance compared to adults. However in Marsh and Northern Harrier, a large proportion was labelled '♀/juv' meaning that they were either adult females or juveniles. 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 one year 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.

The proportion of juveniles at Falsterbo was compared to vole indices from three different places in Sweden (Hörnfeldt 1994, Fig. 1).

Table 1. Annual totals of migrating raptors at Falsterbo 1986–1995. s.d.: standard deviation, CV: coefficient of variation.

Tab. 1. Jahressummen ziehender Greifvögel in Falsterbo von 1986 bis 1995. s.d.: Standardabweichung, CV: Variationskoeffizient.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Average	s.d.	CV (%)	% Aged
Honey Buzzard	6858	3959	6954	7357	3794	2738	7245	4994	4707	3445	5205	1751	34	92
Red Kite	291	243	313	499	452	664	507	706	829	763	527	207	39	88
Marsh Harrier	261	281	444	729	724	915	794	810	775	659	639	229	36	86
Northern Harrier	342	150	180	356	263	261	166	149	160	129	216	84	39	68
Goshawk	30	31	15	19	43	106	79	34	101	32	49	34	69	99
Eurasian Sparrowhawk	15,712	14,722	11,379	16,069	14,439	17,240	9315	12,678	19,881	10,744	14,218	3227	23	8
Common Buzzard	7094	10,770	11,914	13,264	13,410	8251	9279	12,938	11,693	9888	10,850	2182	20	27
Rough-legged Buzzard	1367	1480	852	955	946	837	601	713	751	802	930	281	30	74
Osprey	159	102	249	251	237	266	286	335	305	185	238	71	30	54
Eurasian Kestrel	374	478	388	606	420	609	312	491	402	192	427	127	30	55
Merlin	272	242	228	158	205	183	164	155	215	148	197	42	21	17
Hobby	71	29	36	48	32	39	43	52	45	46	44	12	27	60
Peregrine	28	15	20	28	15	23	26	33	37	28	25	7	28	87

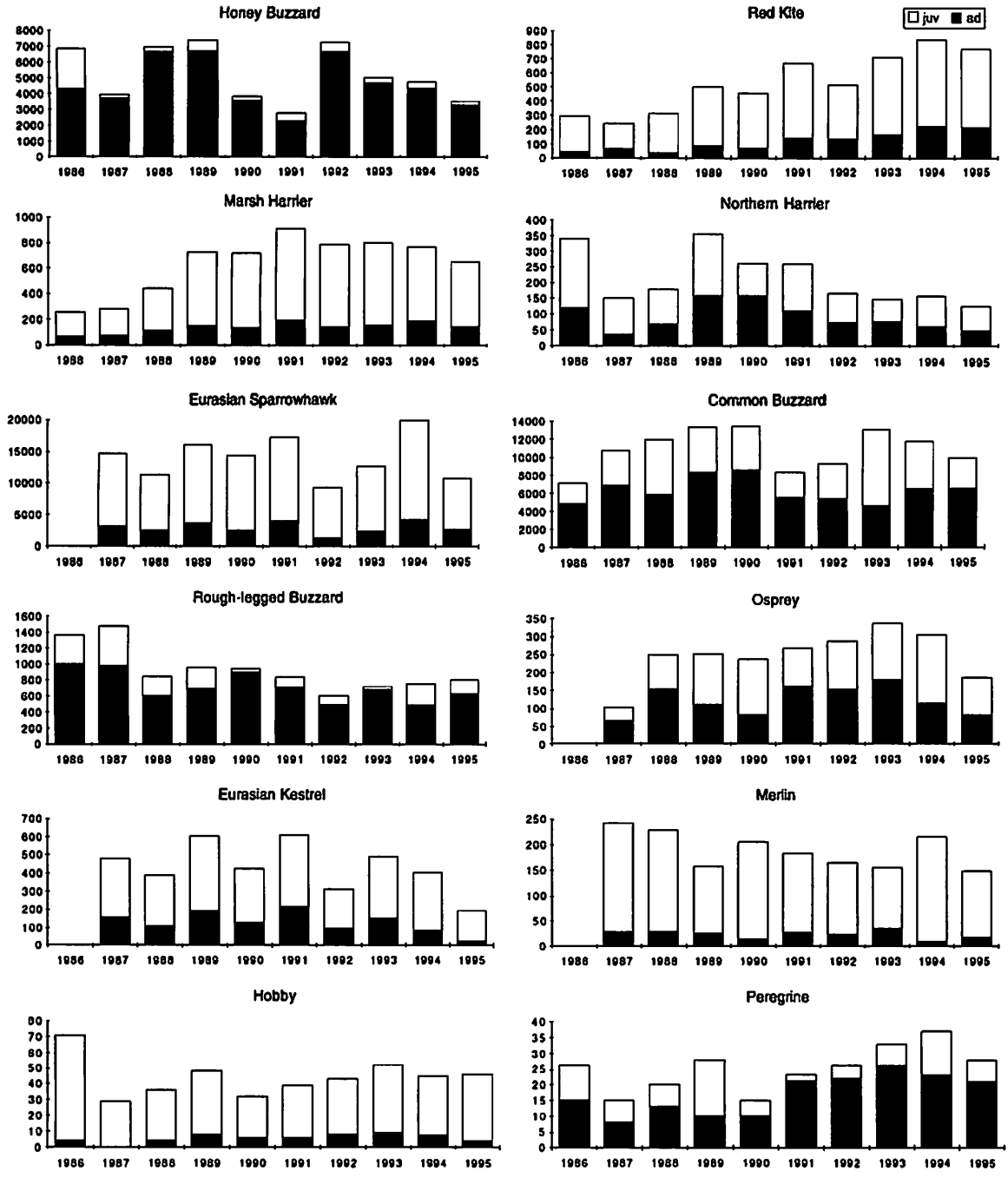

Fig. 2. Annual variation in the number of adult (black) and juvenile (white) migrants at Falsterbo during 1986–1995 in 12 different raptors.

Abb. 2. Jährliche Anzahlen ziehender Greifvögel in Falsterbo zwischen 1986 und 1995. Schwarze Balken: Altvögel; weiße Balken: Jungvögel.

Results and comments for the different species

Annual totals, average, standard deviation, coefficient of variation (CV = s.d./average) and the proportion of individuals aged are presented in Table 1. Only species with an annual average of at least 25 individuals are included. For two species with an annual average of only 10 migrants, the White-tailed Eagle *Haliaeetus albicilla* and Montagu's Harrier *Circus pygargus*, the CV-value was 50 and 52%, respectively. In general, species occurring in low numbers showed the greatest relative variation, while the two most common migrants had comparably low values.

Variation in the annual number of adult and juvenile migrants in twelve different raptors are shown in Fig. 2, while Table 2 depicts variation in the percentage of juveniles over the years. Some species show a constantly high proportion of juveniles, primarily due to a lower concentration of adults at Falsterbo (Kjellén 1997). In these raptors the variation in the proportion of juveniles between different years is rather small and thus hardly reflect the annual production of young. In more uncommon species the high variation is primarily due to small annual totals. A comparison of the coefficient of variation between annual numbers of adults and juveniles for the ten-year period is given in Table 3, while Table 4 presents the number of juveniles/100 migrating adults for six species.

Table 3. Comparison of coefficient of variation (CV, %) between annual numbers of adults and juveniles.
Tab. 3. Vergleich der Variationskoeffizienten (CV, %) jährlicher Anzahlen ziehender Jung- und Altvögel in Falsterbo von 1986 bis 1995.

Species	CV ad.	CV juv.
Honey Buzzard	34	115
Red Kite	57	36
Marsh Harrier	31	38
Northern Harrier	47	41
Goshawk	194	65
Eurasian Sparrowhawk	32	23
Common Buzzard	22	39
Rough-legged Buzzard	26	67
Osprey	34	36
Eurasian Kestrel	47	25
Merlin	35	22
Hobby	48	30
Peregrine	38	59

This is another way of comparing the variation in the annual number of juveniles in species where the ages are more equally concentrated at Falsterbo, and the annual figures may reflect variation in breeding success.

In most raptors it is possible to separate the sexes in adult birds, while the juveniles have only been sexed among Accipiter-hawks and Peregrines *Falco peregrinus*. The proportion of males is given in Table 5. In spite of some annual variation most species show an even sex ratio at Falsterbo over the whole ten-year period. There are, however, some marked exceptions. The annual variation in age and sex

Table 2. Percentage of juveniles among migrating raptors at Falsterbo 1986–1995.
Tab. 2. Prozentualer Jungvogelanteil ziehender Greifvögel in Falsterbo von 1986 bis 1995.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Average	s.d.
Honey Buzzard	37	6	4	9	7	18	8	7	8	6	11	10
Red Kite	84	75	89	83	86	80	75	78	74	74	80	5
Marsh Harrier	74	74	74	79	81	78	82	81	75	77	78	3
Northern Harrier	65	75	62	55	40	58	57	48	61	61	58	9
Goshawk	100	100	93	89	100	84	94	100	99	97	96	6
Eurasian Sparrowhawk		79	78	77	83	77	86	82	79	76	80	3
Common Buzzard	31	36	51	37	36	34	43	65	45	35	41	10
Rough-legged Buzzard	27	34	29	28	6	16	19	5	35	22	23	11
Osprey		26	38	57	66	40	47	47	63	57	49	13
Eurasian Kestrel	70	68	73	68	70	65	71	70	80	88	72	7
Merlin		88	87	83	93	85	86	77	96	88	87	5
Hobby	94	100	89	83	81	85	81	83	82	91	87	6
Peregrine	43	29	35	64	33	4	15	21	38	25	31	16

Table 4. Number of juveniles/100 adults among migrating raptors at Falsterbo 1986–1995.
Tab. 4. Zahl der Jungvögel pro 100 Altvögel bei ziehenden Greifvögeln in Falsterbo von 1986 bis 1995.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Average	s.d.	CV(%)
Honey Buzzard	59	6	5	10	8	22	9	8	9	6	14	16	116
Northern Harrier	190	305	165	124	65	139	131	94	154	158	152	64	42
Common Buzzard	46	57	104	60	57	51	74	188	83	54	77	43	55
Rough-legged Buzzard	36	52	41	38	6	18	24	5	54	29	30	17	57
Osprey		57	62	130	196	66	88	87	170	131	110	50	45
Peregrine	73	88	54	180	50	10	18	27	61	33	59	49	82

ratio for the thirteen most numerous raptor species is commented below.

To investigate underlying causes for the variation in the proportion of juveniles the annual percentages in Table 2 were correlated pairwise in all the involved species. This revealed some positive correlations, most likely related to the food choice. The most obvious covariation in the annual number of juveniles was found among Northern Harriers and Rough-legged Buzzards (Fig. 3). Many raptors are more or less dependent on rodents for their breeding. The annual variation in five northerly species reported to fluctuate with vole numbers (Hagen 1969, C. G. Wiklund pers. comm.) have been compared in Table 6a. In Northern Harrier, Rough-legged Buzzard and Common Buzzard the number of migrating juveniles/100 adults has been used as the best measure of young production. In Eurasian Kestrel and Merlin, with a clear overrepresentation of juveniles at Falsterbo, the annual totals of young birds were used instead. Standardised trapping of voles are performed in three different regions of Sweden (Hörnfeldt 1994 & in lit.). These are Norra Kvill in the province of Småland, Grimsö in Västmanland and Vindeln in Västerbotten (Fig. 1). Published indices reveal the number of caught voles/100 trap-nights during spring and autumn every year. In Table 6b these indices have been correlated with the annual measures of young production in the five raptor species as recorded at Falsterbo.

Honey Buzzard *Pernis apivorus*

The Honey Buzzard is a long-distance migrant spending the winter in tropical Africa. It is the only raptor showing a significant decrease in the annual numbers at Falsterbo during the last twenty years (Roos 1996). The number of adult migrants varied between roughly 2700 and 7400 during the period (Fig. 2). Most likely this reflects the varying concentration to Falsterbo due to the prevailing weather during the pro-

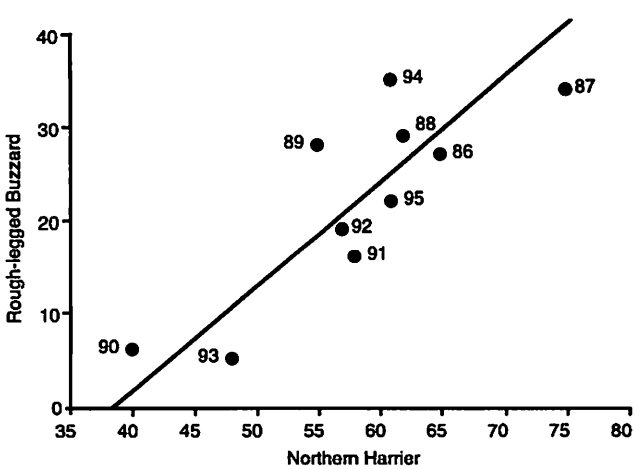

Fig 3. The annual covariation in the percentage of juveniles among migrating Northern Harriers and Rough-legged Buzzards at Falsterbo during 1986–1995. Figures depict the different years. (Regression with major axis line.)

Abb. 3. Jährliche prozentuale Schwankungen der Jungvogelanteile bei Kornweihe und Rauhfußbussard in Falsterbo von 1986 bis 1995 (Regressionsanalyse). Die Zahlen an den Punkten bezeichnen das Jahr.

nounced migration peak in late August. Compared to the other raptors in the study however, the relative variation in number of adult migrants was not especially high (Table 3).

With an average of only 11 percent the proportion of juveniles is the lowest of all species (Table 2). Furthermore the variation in the annual numbers of juveniles is the highest in this study (Tables 3 and 4). The Honey Buzzard is dependent on good numbers of wasp nests to be able to raise young and the productivity is generally low. According to data from continental Europe the production is in the order of 1 young/breeding pair (Newton 1979, Cramp & Simmons 1980), while a study from Central Sweden in 1986–91 revealed only 0.6 young/pair (Tjernberg & Ryttman 1994). Thus the low numbers at Falsterbo are probably to a large degree a result of a poor breeding success in Sweden, although juveniles generally seem to migrate on a broader front and be somewhat less concentrated to the peninsula (Stolt et al. 1992, Kjellén 1997). During the period 1977–95 the only year with a higher number of juveniles at Falsterbo was 1986 (Søgaard & Østerby 1989, Table 2). The next highest proportion of juveniles, in 1991 (18%), is primarily a result of the low number of adults in that year (Fig. 2). If instead compared with the average number of adult migrants in the period the juvenile percentage in 1989 is raised to 13% and that of 1991 descend to 10%, while the changes in the other years are less marked.

Only a proportion of the adults in some years were sexed, but the variation in sex ratio was very small (Table 5). The sample indicates an even sex ratio, with only a slight dominance of males.

Red Kite *Milvus milvus*

The population of Red Kites in southernmost Sweden has undergone a marked increase since the 1970s and was estimated at 650 pairs in 1995 (Kjellén 1996a). This is reflected in the steady growth of numbers at Falsterbo (Fig. 2, Table 1), which explains some of the variation in the annual figures. The comparatively low number of migrating adults is due to a majority of these spending the winter in southernmost Sweden (Kjellén 1994). Part of the older migrants are second year birds not yet sexually mature. These have not generally been separated from adults since this is only possibly under very favourable conditions. The proportion of juveniles (yearlings) has been stable on a high level (Table 2). Since the production of young has been constantly high during the period (Kjellén 1996a), the variation in the annual proportion of juveniles at Falsterbo is most likely dependent on the concentration rate due to more or less suitable weather during the migration peak of the different ages. Juveniles on average leave a week ahead of the adults.

Marsh Harrier *Circus aeruginosus*

Although some of the migrants were labelled ♀/juv it is generally not so difficult to separate

Table 5. Percentage of males among migrating raptors at Falsterbo. Missing values: not sexed in these years.
Tab. 5. Prozentualer Anteil von Männchen bei ziehenden Greifvögeln in Falsterbo von 1986 bis 1995. Leere Felder: keine Geschlechtsbestimmung.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Average	s.d.
Honey Buzzard ad.			53	51	50	52	53	47			51	2
Marsh Harrier ad.	46	33	39	37	48	45	45	42	54	53	44	7
Northern Harrier ad.	36	30	38	38	43	44	36	47	40	32	38	5
Goshawk juv.					61	72	62	79	70	74	70	7
Eurasian Sparrowhawk ad.		51	38	51	41	48	48	46	56	44	47	6
Eurasian Sparrowhawk juv.		62	53	42	44	56	38	37	62	52	50	10
Rough-legged Buzzard ad.				60	53	51	45	49	50	50	51	5
Osprey ad.						46	59	46	54	54	51	6
Eurasian Kestrel ad.		55	41	58	40	47	45	48	45	50	48	6
Peregrine ad.						57	41	58	70	62	58	11
Peregrine juv.							50	57	36	57	49	10

adult females from juveniles and in total 86% of the migrants were aged (Table 1). All Scandinavian Marsh Harriers are migrants spending the winter in the northern half of Africa. The Swedish population is presently in an expanding phase (Kjellén 1996b), as reflected by the higher totals during the second half of the period compared to the first (Table 1). The proportion of juveniles has however been remarkably constant, varying only between 74 and 82% in the ten years (Table 2). Thus the material give no indication of any marked variation in breeding result between years. With an average production around 2 young per breeding pair (Newton 1979, Cramp & Simmons 1980), adults are apparently less concentrated at Falsterbo than juveniles (Kjellén 1997). Most likely older birds are less reluctant to cross larger bodies of open water and thus generally migrate on a broader front.

Contrary to most other species there is a clear dominance of females among the adult Marsh Harriers at Falsterbo (Table 5). Since females on average migrate earlier than males (Kjellén 1992), the variation between single years may be due to different weather conditions during the peak passage of each category. Thus in 1994–95, the two years with a dominance of males (Table 5), the mean passage was later than average at Falsterbo. Since it seems unlikely that males should be less concentrated at Falsterbo than females, the counts indicate a skewed sex ratio in adult Marsh Harriers with 1.27 females per male.

Northern Harrier *Circus cyaneus*

Especially during late autumn when the females have finished moulting of the remiges they are harder to distinguish from juveniles, resulting in a higher proportion of unaged birds compared to the previous species (Table 1). The breeding range is primarily situated in the northern taiga zone. Although small numbers spend the winter in southernmost Sweden, the majority migrate further south in Europe. The annual totals varied slightly more than in the Marsh Harrier (Table 1). Especially the relative variation in the number of adult migrants was larger (Fig. 2). This is probably primarily governed by weather factors although the decreased numbers in recent years seem to be linked to lower rodent numbers in northern Sweden (Hörnfeldt 1994). The relative number of juveniles varied between 65 and 305 per 100 adults (Table 4). Most likely this mirrors the production of young, being governed by rodent numbers in the northern breeding range. Although the proportion of adults is higher among the few birds wintering in southern Sweden (Kjellén 1994), juveniles are probably somewhat more concentrated at Falsterbo than older birds (Kjellén 1997).

The skewed sex ratio in adult birds is even more pronounced than in the Marsh Harrier (Table 5). If the sexes are equally concentrated at Falsterbo the average of 38% males corresponds to a sex ratio of 1.63 females per male! Since the dominance of females was even higher among Northern Harriers wintering in southernmost Sweden (Kjellén 1994) the skewed ratio can not be explained by more males wintering north of Falsterbo.

Goshawk *Accipiter gentilis*

The Goshawk is primarily a resident or short-distance migrant. Only small numbers reach Falsterbo and the annual variation in numbers is comparatively high (Table 1). This may indicate that the number of birds leaving Sweden fluctuates annually due to for instance changes in the breeding success and/or food supply. Ringing recoveries show that adults are more stationary than young birds and that females in general move shorter distances compared to males (Haukioja & Haukioja 1970). This corresponds well with the observations in this study, were adults formed only 4% of the migrants and all of these older birds were males. Also among the juveniles there was a clear dominance of males (Table 5), supporting a more northerly wintering range in young females (Haukioja & Haukioja 1970).

Eurasian Sparrowhawk *Accipiter nisus*

With an average of 14,200 migrants the Eurasian Sparrowhawk was the most common raptor at Falsterbo during the period (Table 1). Although northern Sweden is vacated in wintertime the species is a fairly common winterer in the southern third of the country. The number of adults varied relatively much between

roughly 1300 and 4100 birds per year. Since a large proportion of the adult Sparrowhawks spend the winter in Sweden this may explain part of this variation as well as the dominance of juveniles at Falsterbo. A possible contributing cause for the relatively low proportion of adults is that they become less concentrated at Falsterbo than juveniles. The variation in the proportion of juveniles was remarkably small around the average of 80 percent (Table 2), which may indicate a stable breeding result in the period. Compared to other species the variance in number of juveniles during the ten years was low (Table 3).

It is possible to separate the sexes in both age categories of Sparrowhawk. The relatively large variation in sex ratio between different years (Table 5) is primarily due to different timing of the migration. In juveniles the migration peak of the sexes is separated by more than two weeks (Kjellén 1992), causing annual differences in the sex ratio due to shifting weather conditions during the respective culmen. In spite of the large annual variation the overall sex ratio was completely even. This can be compared to 51% males in a large British study (Newton & Marquiss 1979). The migration peaks do not differ as much in adults and the differences in sex ratio between years was smaller. The somewhat higher average percentage of adult females at Falsterbo could possibly indicate that more of the males winter in Sweden, but I have not seen any data to support this. Instead females have been found to winter generally north of males in Eurasian Sparrowhawk (Belopolskij 1971, Cramp & Simmons 1980), as well as the American counterpart Sharp-shinned Hawk *A. striatus* (Clark 1985).

Common Buzzard *Buteo buteo*

The majority of Swedish Common Buzzards migrate to western Europe, and only in the southernmost province (Scania) is the species common in winter (Alerstam 1990). The proportion of adults is higher among those wintering compared to the migrants at Falsterbo (Kjellén 1994). With figures between roughly 7100 and 13,400 migrants, the relative variation in annual totals is the lowest in Table 1. This implies a fairly stable concentration rate at Falsterbo in this species, being highly dependent on thermal migration. Comparing the ages shows a higher variation in juvenile numbers than in the number of adult migrants (Table 3). This is also demonstrated by the comparatively high variation in the number of juveniles/100 adults (Table 4). The average of 77 juveniles/100 adults corresponds to an annual production in the order 1.0–1.5 young/pair (Newton 1979, Cramp & Simmons 1980), indicating that old and young buzzards are about equally concentrated at Falsterbo. Thus the variation in the relative number of juveniles (Table 4) may well reflect the annual breeding result. However, since the migration median of the ages is separated by about ten days (Kjellén 1992), part of the differences between years is likely to be caused by varying concentration to the peninsula due to weather conditions during the respective peak.

Rough-legged Buzzard *Buteo lagopus*

The Rough-legged Buzzard is like the Northern Harrier a northern species dependent on the fluctuating number of rodents (Alerstam 1990). Small numbers winter in southern Sweden, but the majority migrate to Central Europe (Dobler et al. 1991). The variation in annual numbers during the period was moderate (Table 1). Fig. 2 indicate a decrease in the number of adult migrants during the period, most likely due to the lack of peak rodent years in northern Scandinavia since 1982 (Hörnfeldt 1994 & in lit.). The number of juveniles fluctuated between 33 and 505 birds, forming an average of 23 percent of the total (Table 2). This reveals a rather low production of young during the ten years. The variance in the annual total of young birds (Table 3) as well as in number/100 adults (Table 4) was comparatively high. Most likely the proportion of young would be higher in a peak rodent year when up to two young/pair may be raised (Hagen 1952, Pasanen 1972).

Among adults, the sexes and second-year birds (born the year before) have been generally separated from 1989 and onwards. Overall the sex ratio seems to be even with 51% males in the whole material (Table 5). The proportion of second-year birds varied between 1 and 12 percent in the seven years, with an average of 6 percent. As might be expected this proportion was positively correlated with the percentage of

juveniles in the preceding year ($r = 0.54$, $p > 0.05$), but the correlation coefficient was not statistically significant.

Osprey *Pandion haliaetus*

The Osprey is a long-distance migrant, spending the winter south of the Sahara (Österlöf 1977, Poole 1989, Saurola 1995). With an estimated population of 3200 pairs in Sweden (SOF 1990), an average of only 238 migrants during the period (Table 1) shows a very low concentration at Falsterbo (Kjellén 1997). Ospreys are good flyers migrating on a broad front, and less reluctant to make longer sea crossings compared to most other raptors. The variation in annual numbers is most likely due to the prevailing weather during the migration peak in late August, although a slight increase may be discerned in Table 1. The rather high differences in the proportion of juveniles between years (Tables 2 and 4) may be related to the breeding result.

Although the plumage of males and females are somewhat variable, adults were sexed as far as possible in the last five years of the study (Table 5). In spite of some annual variations the overall sex ratio seems to be even, with an average of 51% males.

Eurasian Kestrel *Falco tinnunculus*

Most Scandinavian kestrels migrate to western and southwestern Europe (SOF 1990). The annual totals varied between approximately 200 and 600 birds (Table 1, Fig. 2), most likely due mainly to weather conditions resulting in varying concentration to the Falsterbo peninsula. Available figures from Scandinavia show an average of around 2.5 fledged young/breeding pair (Kjellén 1997). The percentage of juveniles remained very high around the average of 72% (Table 2), giving no real clues to variations in the production of young. Although the proportion of adults is higher among the few wintering birds (Kjellén 1994), their numbers are not large enough to explain the dominance of juveniles at Falsterbo. Instead it is likely that adult kestrels are generally stronger flyers and thus migrate on a broad front (without being concentrated at Falsterbo) to a higher degree than young birds.

The slight dominance of females among the adults in Table 5 may, at least partly, be explained by a higher tendency for males in pairs nesting in southernmost Sweden to spend the winter close to the breeding site (Wallin et al. 1985, Kjellén 1994).

Merlin *Falco columbarius*

The Merlin is primarily a bird of the northern mountains. Although a few birds are seen in southernmost Sweden every winter, the great majority migrate to western Europe. The variation in annual numbers was lower than in most other species (Table 1). The constant dominance of juveniles is even more pronounced than in the previous species, with an average as high as 87 percent (Table 2). It is uncertain whether the totals provide any indication of the breeding success, in that case suggesting fairly low annual differences in the production of young within the period (Table 3).

Hobby *Falco subbuteo*

All Hobbies are tropical migrants, spending the winter south of the Sahara. With an average of only 44 migrants in the period, the Hobby is fairly uncommon at Falsterbo (Table 1). Since the Swedish population has been estimated at 1000 pairs (SOF 1990) the concentration to the peninsula is obviously very low (Kjellén 1997). Like in the other small falcons, juveniles dominated to a very high degree with between 81 and 100% of the annual total (Table 2), indicating that adults generally migrate on a broader front. As in the two other small falcons the annual figures may possibly indicate a fairly constant breeding result during the ten years (Table 3).

Peregrine *Falco peregrinus*

The recent increase in the small Swedish population of Peregrines (Ahlén & Tjernberg 1996) is reflected in the counts from Falsterbo (Table 1), but the species is still quite an uncommon migrant. The average of 31% young birds (Table 2) is much lower than in the small falcons. Only a few Peregrines winter in Sweden, and thus obviously adults are proportionally more concentrated at Falsterbo compared to the smaller species (Kjellén 1997). This is somewhat surprising since adult Pere-

grines are very strong flyers, migrating even in windy and rainy conditions. They would thus seem likely to avoid concentration points as Falsterbo to a greater degree than juveniles. Primarily due to small annual numbers the percentage of juveniles fluctuated greatly during the period (Tables 3 and 4).

Peregrines have been sexed since 1991 (Table 5). The high variation in the proportion of males is most likely caused by the small annual numbers. Not to much weight should thus be placed on the average dominance of males among the adults, especially since the percentage was more even in juveniles.

General discussion

Variation in age ratio

Generally species occurring in low annual numbers showed a greater relative variation (Table 1). The extremely high variation in Goshawk numbers may be caused by varying numbers of this primarily resident species leaving Sweden due to fluctuations in the food supply. In Red Kite and Marsh Harrier the comparatively high percentages are mainly the result of a marked increase in population numbers during the period. At the other end Merlin and Hobby may be noted for a relatively low variation in annual numbers. The reason for this may be that they are less dependent on thermal migration and thus less affected by variation in weather conditions. An alternative or contributory explanation would be a comparatively stable production of young in the period.

The average percentage of juveniles varied a lot between different species (Table 2). Goshawk has an almost total dominance of young birds since the adults are resident. Also in Red Kite and Eurasian Sparrowhawk is the very high proportion of juveniles due to a greater number of old birds spending the winter in Sweden. In Marsh Harrier and the three small falcons on the other hand, where the great majority of both adults and juveniles are migrants, the overrepresentation of juveniles at Falsterbo may instead be explained by a lower tendency of adults to follow leading lines and thus pass migration concentration points. All the above mentioned seven species are characterised by a low standard deviation (Table 2). The relatively constant proportion of juveniles give no good indication of annual variation in the production of young (Table 3). Either the production was on a steadily high level or more likely cannot be discerned in the counts from Falsterbo.

In Northern Harrier and Osprey the domination of juveniles is less extreme and the variation between years greater, thus more likely reflecting the breeding result. However, numbers of juveniles/100 adults fluctuated less than the other species in Table 4. The Common Buzzard had more even proportions between the ages with fairly high annual differences, especially in the number of juveniles (Table 3). The annual variation was even larger in Rough-legged Buzzard although the proportion of juveniles was roughly only half as high. Thus the production of young during the period seems to have been significantly lower in Rough-legged Buzzard as compared to Common Buzzard. The high annual variations in the proportion of juvenile Peregrines is almost certainly primarily an effect of the small annual totals. The extremely low numbers of young Honey Buzzards (Table 2) can be assumed to reflect a very low annual juvenile production, as reported from Sweden (Tjernberg & Ryttman 1994).

Correlations between different vole-dependent raptor species and their prey

The most obvious positive correlation in the annual variation in the percentage of juveniles is the one between Northern Harrier and Rough-legged Buzzard ($r = 0.83$, $p < 0.01$). Both are northerly species breeding in the mountains and taiga of northern Scandinavia. They are highly dependent on rodents (primarily voles and lemmings) and the breeding result fluctuates annually due to variation in prey numbers (Watson 1977, Alerstam 1990). In years when voles were very scarce Rough-legged Buzzards near Dovre, in Norway neither took up territories, nor formed pairs (Hagen 1969). It thus seems very likely that the correlation in the proportion of juveniles is governed by the annual fluctuations in the quantity of rodents. This is only partly supported by the vole figures from Northern Sweden (Table 6B). The vole indices were obtained in the coniferous zone, which may explain the better corre-

lation with Northern Harrier. Most likely rodent figures from the mountain region would show a better correlation with Rough-legged Buzzard numbers. The connection between the two species can also be illustrated by a regression (Fig. 3), where the different years are depicted. According to this 1987 produced the highest number of young, while the breeding result was poorest in 1990. It may be noted that during the period there was no pronounced peak in rodent numbers. Also the rodent numbers are not necessarily synchronised over the whole breeding range. Thus in 1994, the year with the highest percentage of young Rough-legged Buzzards at Falsterbo, no high numbers were found in the mountains of northern Sweden, while there was a local peak of lemmings in the mountains of southern Norway (Göran Högstedt pers. comm.). The generally higher percentage of juveniles in Northern Harrier (Fig. 2) can be explained by a proportionally lower concentration of adults at Falsterbo, but perhaps also by a higher average juvenile production (Newton 1979, Cramp & Simmons 1980).

In southern Norway the breeding success of Northern Harrier, Rough-legged Buzzard, Eurasian Kestrel and Merlin was more or less affected by vole densities, while Honey Buzzard and Osprey were unaffected (Hagen 1969). Northern Harrier and Eurasian Kestrel are both rodent specialists primarily found in the coniferous region, so a food connection is likely. Rough-legged Buzzard and Merlin are more connected with the mountainous region of Scandinavia. Although the latter take mainly birds, several studies indicate that the breeding result is generally better in rodent years (Hagen 1969, C. G. Wiklund pers. comm.). Hagen's study indicate a relationship between rodent numbers and young production in all the four raptor species above. There is a significant correlation in the annual juvenile variation at Falsterbo between Northern Harrier as well as Rough-legged Buzzard and Merlin (Table 6A).

Table 6. Comparison of number of juveniles/100 adults in Northern Harrier, Rough-legged Buzzard and Common Buzzard, and of total number of juveniles in Eurasian Kestrel and Merlin respectively, among migrants at Falsterbo. **A:** Spearman rank correlation coefficients of the annual figures 1986–1995 for the five species. (* = $P < 0.05$). **B:** Correlation coefficients with spring (S) and autumn (A) vole indices from three different regions of Sweden during the period 1986–1995. The limit for statistical significance ($p < 0.05$) is at corr. coeff. > 0.63, and thus none of these correlations reach statistical significance.

Tab. 6. Vergleich der Jungvogelanteile pro 100 durchziehender Altvögel bei Kornweihe, Rauhfußbussard und Mäusebussard, sowie Gesamtzugzahlen junger Turmfalken und Merline in Falsterbo. **A:** Spearman Rangkorrelationskoeffizienten der jährlichen Zugzahlen für fünf Arten von 1986–1995 (* = $p < 0{,}05$). **B:** Korrelationskoeffizienten und Kleinnager-Indices aus Herbst (A) und Frühjahr (S) für drei verschiedene Gebiete in Schweden von 1986 bis 1995. Die Grenze für statistische Signifikanz ($p < 0{,}05$) wird bei einem Korrelationskoeffizienten von > 0,63 erreicht; daher erreicht keiner dieser Korrelationskoeffizienten statistische Signifikanz.

A

	R.-leg. Buz.	Com. Buz.	E. Kestrel	Merlin
Northern Harrier	0.68*	–0.38	–0.32	0.65*
Rough-legged Buzzard		–0.02	–0.02	0.60*
Common Buzzard			0.05	–0.38
Eurasian Kestrel				–0.13

B

Species	Norra Kvill		Grimsö		Vindeln	
	S	A	S	A	S	A
Northern Harrier	0.33	–0.10	0.17	0.44	0.62	0.38
Rough-legged Buzzard	0.30	0.10	0.29	0.19	0.29	0.19
Common Buzzard	–0.30	0.40	0.13	–0.04	–0.31	–0.54
Eurasian Kestrel	0.08	0.06	0.09	0.31	–0.17	–0.32
Merlin	0.33	0.48	0.56	0.58	0.38	0.48

This supports a food connection in these three northerly species primarily found in the taiga zone, while the Eurasian Kestrel does not seem to follow the same pattern. One reason may be the constantly high proportion of juveniles in the small falcons due to a lower concentration of adults at Falsterbo. If we instead compare the annual number of juvenile migrants, there is a weaker positive correlation between Northern Harrier and Eurasian Kestrel indicating a similar food relation. Although the Common Buzzard takes mainly rodents, the lack of covariation with the other species in Table 6 may be due to the majority of the Common Buzzards nesting in the southern half of Sweden, with a generally less fluctuating food supply (Hansson & Henttonen 1988). There is a clearly higher general tendency of positive correlations to vole numbers in the three northern species Northern Harrier, Rough-legged Buzzard and Merlin as compared to Common Buzzard and Eurasian Kestrel, with a large part of the population in the southern half of Sweden (Table 6B).

Variation in sex ratio

Most studies of the sex ratio of raptors in the nest have found the sexes to occur in proportions close to 50:50, although the ratio among migrating and wintering birds varied considerably more (Newton 1979). This may be explained by differences in migratory behaviour or separated winter quarters between the sexes. This study of migrants at Falsterbo shows a ratio close to 50:50 in most species (Table 5). The clear dominance of males among the young Goshawks can be assumed to depend on the tendency for females to generally winter north of males (Haukioja & Haukioja 1970, Mueller et al. 1977). An extensive material from Great Britain shows an even sex ratio among nestlings in Eurasian Sparrowhawk, with 51% males (Newton & Marquiss 1979). This is supported by the even average among juveniles at Falsterbo. The slight overall dominance of adult females may be a result of the large annual variation in numbers, or possibly because more males (having a somewhat later migration culmen) pass after the counts end on 20 November. In general, species with a larger difference in median date between the sexes at Falsterbo show a larger standard deviation in Table 5 ($r = 0.47$, $n = 11$, $p > 0.05$).

A higher proportion of males among the adult Peregrines at Falsterbo is most likely to be an effect of the small annual totals (Table 1). Although most kestrels are migrants, an average slight dominance of females may be attributed to more males among the minority spending the winter in southernmost Sweden (Wallin et al. 1985, Kjellén 1994).

There are two species where the markedly skewed sex ratio observed at Falsterbo cannot be explained by different wintering or migration strategies. These are Marsh and Northern Harrier with an average ratio of 1.27 and 1.63 females/migrating male, respectively (Table 5). Since females culminate ahead of males at Falsterbo in both species (Kjellén 1992), differences in proportion between single years may be due to varying weather conditions during the respective migration peak. However, the overall dominance of females in the ten years seems obvious. Overrepresentation of one age category is often assumed to be caused by a greater tendency to follow leading lines and thus to concentrate at Falsterbo. I can however see no reason why male harriers in general should migrate on a broader front and thus avoid the peninsula to a higher degree than females.

The sex ratio among fledglings of Marsh Harrier, after mortality among eggs and nestlings, was male biased in two studies from the Netherlands (Zijlstra et al. 1992, Bijlsma 1993). Also in Northern Harrier, data from the Netherlands indicate more males among fledglings (Bijlsma 1993). On the other hand a large material from the Orkney Islands, Scotland showed a significantly higher proportion of females among the nestlings (53.6%), equal to a ratio of 1.16 females/males ($n = 1061$, Balfour & Cadbury 1979). Also in SW Scotland females dominated with a ratio of 1.47 females per male among 42 young Northern Harriers (Watson 1977). Thus in this species a skewed sex ratio in favour of females is found already in the nest at least in some regions. There are few reliable figures on the actual ratio among adult birds either from the wintering or the breeding range. Local differences in sex ratio among wintering raptors can usually be explained by separate winter

habitat and/or range (e.g. Haukioja & Haukioja 1970, Marquiss & Newton 1979, Arnold 1991).

Like other harriers both Marsh and Northern Harriers are often polygynous (Newton 1979, Cramp & Simmons 1980). In parts of the Netherlands polygyny in Marsh Harrier is quite common (Bijlsma 1993) but the phenomenon seems to be somewhat less widespread in Sweden (Bengtson 1967, Kjellén 1996b). The highest frequency in Northern Harrier has been reported from Scotland, were 58 percent of the males were polygynous (Balfour & Cadbury 1979). Polygyny is also fairly frequent in the Netherlands (Bijlsma 1993). Although breeding already in the second year is more frequent among females than males in both harriers (Glutz von Blotzheim et al. 1971, Balfour & Cadbury 1979), only small numbers normally breed already in their second year. It is possible that the proportion of females in the population among adult raptors is reflected in the rate of polygyny. Thus the relatively high tendency for polygyny in harriers may possibly be the result of an excess of adult females as found among the migrants at Falsterbo.

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