

DIFFERENCES IN AGE AND SEX RATIO AMONG MIGRATING
AND WINTERING RAPTORS IN SOUTHERN SWEDEN

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ABSTRACT.—In order to test hypotheses explaining intraspecific differences in migration patterns of birds, a four-year field study of migrant raptors in southernmost Sweden was undertaken. The age and sex ratios among autumn migrants departing from the province of Scania at Falsterbo were compared to the corresponding ratios among birds of the same species that stayed in Scania the following winter. In most species (Red Kite [*Milvus milvus*], White-tailed Eagle [*Haliaeetus albicilla*], Northern Harrier [*Circus cyaneus*], Goshawk [*Accipiter gentilis*], Sparrowhawk [*A. nisus*], Common Buzzard [*Buteo buteo*] and Eurasian Kestrel [*Falco tinnunculus*]), the proportion of adults was distinctly higher among wintering birds than among the migrants. A marked exception was the Rough-legged Hawk (*B. lagopus*), which had significantly more juveniles among the wintering birds. In most species where the sexes could be separated more females were found among the wintering birds than among the migrants (Northern Harrier, Goshawk, Sparrowhawk and Rough-legged Hawk). The Eurasian Kestrel, however, showed the reverse pattern with a higher proportion of males among wintering birds. The results support the social-dominance hypothesis, where the dominant adults and the larger sex (in raptors the female) generally winter furthest north. That juveniles are driven away from the breeding territories is suggested by a significantly higher proportion of juvenile Common Buzzards wintering in marginal coastal regions as compared to the inland portion of Scania. The results are also in general agreement with Bergmann's rule. The higher proportion of male Eurasian Kestrels among wintering birds is most likely explained by the importance of early arrival at the breeding territory. Received 6 July 1992, accepted 25 November 1992.

AMONG BIRDS we find a mixture of migration strategies from completely resident species to long-distance migrants travelling thousands of kilometers between summer and winter quarters each year. Migration can be expected to occur in populations where birds survive in greater numbers if they leave their breeding areas for the nonbreeding season than if they remain there for the whole year (Lack 1954). Even within species there may be great variation. In the Common Buzzard (*Buteo buteo*), birds breeding in northeast Europe are long-distance migrants spending the winter in southern Africa, while birds breeding in most parts of Scandinavia are short-distance migrants wintering on the European mainland, and breeding birds in southern and western Europe are residents (Cramp et al. 1980). Within species, various categories of birds (e.g. age and sex classes) clearly have different migration patterns. This so-called differential migration has attracted the attention of several authors (Gauthreaux 1982, Ketterson and Nolan 1983, Lundberg 1988). Several hypotheses have been put forward to explain inter- and especially intraspecific differences in

migratory and wintering patterns in birds. Compilations have been made by Gudmundsson (1988) and Kerlinger (1989) and a short summary follows: (1) The body-size hypothesis, closely related to Bergmann's rule (Salomonsen 1955), states that large birds are able to winter further north since they are better able to tolerate cold surroundings (Searcy 1980). As a result, smaller individuals can be expected to undertake longer migrations than larger ones. (2) The social-dominance hypothesis (Cox 1968, Mueller et al. 1977, Gauthreaux 1978, 1982) proposes that, in short-distance migrants, subordinate individuals are forced to migrate from the breeding grounds (and/or the best wintering areas) because of competition from more dominant birds. (3) The arrival-time hypothesis (King et al. 1965, Myers 1981) indicates that, if there is competition for breeding resources, birds returning earlier to the breeding grounds do better. Therefore, it is advantageous to winter as close to the breeding area as possible. (4) The character-divergence hypothesis (Koplin 1973) explains differences in winter habitat as being a result of character displacement due to

differences in prey selection. (5) The migration-cost hypothesis (Pienkowski and Evans 1985, Pienkowski et al. 1985) states that, if migration cost (which may vary with age and sex) is very high, birds should minimize the distance between the breeding and wintering areas. (6) Flight energetics have also been suggested to explain migratory patterns (Gudmundsson 1988). Smaller birds use less energy per flight distance and, thus, may be more capable of migrating long distances.

The six hypotheses outlined above are not mutually exclusive and a combination of factors is likely to affect differential migration. Other hypotheses like the feeding-efficiency hypothesis (Rosenfield and Evans 1980, Duncan 1982) and molt hypothesis (Smallwood 1988, Kerlinger 1989) are mainly concerned with the onset and timing of migration rather than the geographic differences between age categories, while the spring-predictability hypothesis (Alerstam and Högstedt 1980) applies to different breeding populations and not to age and sex categories.

Most studies of differential migration until now have been based on banding recoveries. Raptors are fairly easy to study in the field, and the development of better binoculars and telescopes and publication of advanced field guides have made it possible to determine the age and sex of individual birds in many cases. The reversed sexual dimorphism of raptors makes them especially interesting to study in view of the different hypotheses about the causes of differential migration.

Scania, the southernmost province of Sweden, is rich in breeding and wintering raptors; in autumn, a spectacular migration is concentrated over the region. Most short-distance migrants among these raptors show a so-called partial migration, where part of the Scandinavian population migrates south in autumn, while a varying fraction winters in southern Sweden. To study the differential migration of these raptors, the proportion of different ages and sexes among autumn migrants was compared to the corresponding proportions among birds staying in Scania the following winter.

METHODS

The migration of raptors at Falsterbo, the southwesternmost point of Scandinavia (Fig. 1), was quantified on the basis of visual counts made by one or

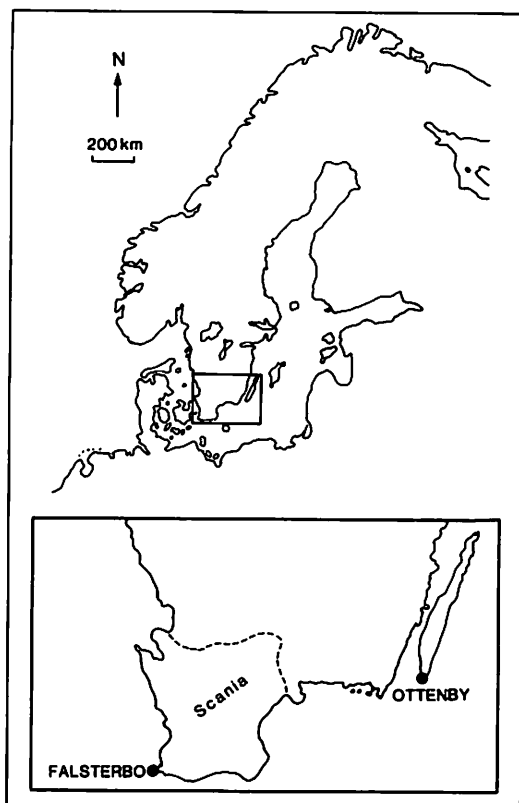


Fig. 1. Study area in southernmost Sweden. Lower panel shows details of rectangular area in upper panel.

two observers from the beginning of August until mid-November in the years 1986–1991. Observers used 10×40 binoculars and wide-angle 30×70 telescopes. Migrants were aged and sexed as far as possible using characters given by Forsman (1984) and Gensböl (1984). Total proportions of different sex and age classes were estimated for each species on the basis of samples of identified individuals (with respect to age and sex), weighted by the total number of individuals during 10-day periods. A more thorough description of methods is given in Kjellén (1992), who analyzed the differential seasonal timing of the raptor migration during the first five years. Differences in the degree of concentration at Falsterbo, with respect to particular age and sex categories, among the migrating raptors cannot be excluded, as discussed by Kjellén (1992).

Studies of wintering raptors in Scania (Fig. 1) were conducted during the months December–February in the four winters 1987/1988–1990/1991. Two observers separately made a great number of excursions by car. Observed raptors were identified as far as possible with respect to age and sex. Individuals observed at the same locality (normally within 1 km of an earlier observation) more than once were considered to be

TABLE 1. Numbers (percents in parentheses) of adults and juveniles of Red Kites and Common Buzzards among migrants at Falsterbo in autumn 1987–1990, and among birds wintering in Scania the following winter.

Year	Migrants			Wintering birds		
	Adult	Juvenile	Total	Adult	Juvenile	Total
Red Kite						
1987	61 (25)	182 (75)	243	159 (88)	21 (12)	180
1988	34 (11)	279 (89)	313	43 (90)	5 (10)	48
1989	84 (17)	415 (83)	499	60 (92)	5 (8)	65
1990	64 (14)	388 (86)	452	70 (89)	9 (11)	79
Total	243 (16)	1,264 (84)	1,507	332 (89)	40 (11)	372
Common Buzzard						
1987	6,848 (64)	3,922 (36)	10,770	167 (82)	36 (18)	203
1988	5,850 (49)	6,064 (51)	11,914	106 (73)	39 (27)	145
1989	8,298 (63)	4,966 (37)	13,264	135 (82)	29 (18)	164
1990	8,525 (64)	4,885 (36)	13,410	160 (79)	42 (21)	202
Total	29,521 (60)	19,837 (40)	49,358	568 (80)	146 (20)	714

identical and are only counted once in the yearly total. Detailed notes on the locality of each observation reduce the likelihood of individuals being counted more than once in a single year. The number of field days each winter was in the order of 30. Excursions were made all over Scania, with a clear concentration in the southern part. Most excursions were made in open or semiopen habitats, meaning that the number of observed individuals of *Accipiter* species

(mainly occurring in closed forest) was low. Generally, no separation of different habitats was made except for a distinction between coastal and inland habitats for Common Buzzards. Observations for each species were summarized by age and sex each winter. Under unfavorable conditions it is not possible to separate females from juveniles in the Northern Harrier (*Circus cyaneus*) and the Eurasian Kestrel (*Falco tinnunculus*). Such birds were labelled "female/juvenile" and, in the tables, they were divided between females and juveniles according to the proportion found in the sample of identified birds. For example, if 60% of all identified females and juveniles were females, the same percentage of the birds in the unidentified group was considered to be females.

TABLE 2. Numbers (percents in parentheses) of adults, immatures and juveniles of White-tailed Eagles, Goshawks, and Sparrowhawks among migrants at Falsterbo in autumn 1986–1991, and among birds wintering in Scania 1987/1988–1990/1991.

Age	Migrants	Wintering birds
White-tailed Eagle		
Adult	3 (7)	11 (24)
Immature	25 (54)	23 (51)
Juvenile	18 (39)	11 (24)
Total	46	45
Goshawk		
Adult male	16 (7)	3 (6)
Adult female	0 (0)	3 (6)
Juvenile male	131 (60)	21 (43)
Juvenile female	72 (33)	22 (45)
Total	219	49
Sparrowhawk		
Adult male	7,843 (11)	21 (32)
Adult female	8,117 (11)	24 (36)
Juvenile male	28,628 (40)	11 (17)
Juvenile female	27,733 (38)	10 (15)
Total	72,321	66

To increase the sample size for wintering Sparrowhawks (*Accipiter nisus*), I used collection data from the Zoological Museum in Lund, in addition to the field observations. All Sparrowhawks in the collection obtained from Scania during the winter months (December–February) were aged and sexed.

Differences in proportions of various categories between migrating and wintering populations were tested statistically with chi-square tests (Siegel 1956). In these tests, only birds of known sex and age were considered.

RESULTS AND COMMENTS

Results are presented in tabular form, and comments on each species are given below. A few species observed in very small numbers during the four winters were excluded from the analyses. In the tables the numbers of wintering birds are given after the figures from the previous autumn. For infrequently observed spe-

TABLE 3. Numbers (percents in parentheses) of males, females and juveniles of Northern Harriers and Eurasian Kestrels among migrants at Falsterbo in autumn 1987–1990, and among birds wintering in Scania the following winter.

Year	Migrants				Wintering birds			
	Male	Female	Juvenile	Total	Male	Female	Juvenile	Total
Northern Harrier								
1987	11 (7)	26 (18)	113 (75)	150	7 (18)	17 (45)	14 (37)	38
1988	26 (15)	42 (23)	112 (62)	180	8 (27)	15 (50)	7 (23)	30
1989	60 (17)	99 (28)	197 (55)	356	2 (9)	15 (65)	6 (26)	23
1990	68 (26)	91 (35)	104 (40)	263	10 (35)	12 (41)	7 (24)	29
Total	165 (17)	258 (27)	526 (55)	949	27 (23)	58 (49)	34 (28)	120
Eurasian Kestrel								
1987	85 (18)	69 (14)	324 (68)	478	20 (49)	11 (27)	10 (24)	41
1988	42 (11)	63 (16)	283 (73)	388	24 (33)	22 (31)	26 (36)	72
1989	111 (18)	81 (13)	414 (68)	606	45 (63)	23 (32)	4 (6)	72
1990	50 (12)	76 (18)	294 (70)	420	31 (41)	20 (26)	25 (33)	76
Total	288 (15)	289 (15)	1,315 (70)	1,892	120 (46)	79 (30)	62 (24)	261

cies, only the summarized total from all four winters and from six autumns at Falsterbo are given.

Red Kite (*Milvus milvus*).—Once a pure migrant, the Red Kite began to winter in Scania in the late 1950s (Ulfstrand 1963). The northward shift of the wintering range in Europe has been attributed to an increase in garbage dumps (Juillard 1977). In connection with a rapid growth in population in recent years, the numbers of migrants at Falsterbo, as well as of wintering birds in Scania, have increased markedly. A census conducted by the Scanian Ornithological Society in January 1991 found approximately 500 kites, with over 200 birds in the largest roost.

Most of the wintering birds are adults (Table 1). The proportion of juveniles seems to vary little among years, staying near the average of 11%. A very large part of migrating Swedish Red Kites passes through Falsterbo in the autumn (Rudebeck 1950). Juveniles dominate strongly with an average of 84% in the four autumns (Table 1). The age distributions of migrating and wintering kites are markedly different ($X^2 = 716$, $df = 1$, $P < 0.001$, $n = 1,683$). Most likely the changed wintering habits of the adult kites have contributed strongly to the marked increase in the Swedish population.

White-tailed Eagle (*Haliaeetus albicilla*).—The White-tailed Eagle assumes a number of plumages before reaching full adult plumage in its fifth or sixth winter (Forsman 1984, Helander et al. 1989). We distinguished among adults, immatures and juveniles. Most immatures were

in their second or third year, but the sample is too small to be separated further. The species is a regular but scarce winter visitor to Scania. Only small numbers migrate further south, which is reflected by the total of only 46 birds recorded in six autumns at Falsterbo (Table 2).

Immatures made up the majority of migrants, as well as wintering birds. The proportion of adults was higher among the wintering birds than among the migrants, while the opposite was true for juveniles (Table 2). There were no significant differences between age categories in the total sample ($X^2 = 4.87$, $df = 2$, $P < 0.10$, $n = 84$). However, if only adults and juveniles are compared, there is a significant difference ($X^2 = 4.83$, $df = 1$, $P < 0.05$, $n = 40$) between the composition of migrating and wintering birds. Most adults in the western Palearctic outside Russia are residents while juveniles and immatures wander mainly south to southwest (Cramp et al. 1980, Gensböl 1984).

Northern Harrier (*Circus cyaneus*).—Adult males, adult females and juveniles were distinguished. In Scandinavia the Northern Harrier is a bird of the northern coniferous zone. Most birds spend the winter on the European continent but small numbers winter in southern Sweden. The breeding success of the species is heavily dependent on rodent numbers (Watson 1977, Alerstam 1990), and the comparatively high among-year variation in the proportion of juveniles among migrants (Table 3) most likely reflects varying breeding results. There probably is a connection between the percentage of juveniles among autumn migrants and winter-

ing birds the following winter, although the correlation is not significant ($r = 0.78$, $P = 0.2$, $n = 4$).

With an average of 55%, juveniles were clearly predominant among the migrants (Table 3). In contrast the proportion of young birds was lower among wintering birds (average 28%). The differences in age and sex composition between migrants and wintering birds is significant in the whole material ($X^2 = 34$, $df = 2$, $P < 0.001$, $n = 1,069$), and the difference in age composition is also significant when comparing only the proportions of adults and juveniles ($X^2 = 16$, $df = 1$, $P < 0.001$, $n = 693$). This indicates that adults generally winter further north than do first-year birds. Most other studies have not distinguished adult females from juveniles, so it is only possible to compare the proportion of adult males. At roosts in the Lake Dümmer area, in northwestern Germany adult males comprised 7% of the population in the winter of 1988/1989 and 19% the following winter (Helbig et al. 1992), while Ludwig et al. (1986) found an average of 25% adult males in the same area from 1970–1985. Both studies indicated large variation in the proportion of males among years. Clarke and Watson (1990), on the other hand, found no differences between years in a large sample from British roosts. However, there was a significantly higher proportion of adult males in western (40%) as compared to eastern (30%) Britain in January.

According to Watson (1977), females on average winter north of males in North America. That this may also be the case in Europe is indicated by the fact that females constituted 61% of the adult migrants at Falsterbo versus 69% of the adults wintering in Scania, although the difference is not significant ($X^2 = 1.74$, $df = 1$, $P < 0.20$, $n = 509$). The biased sex ratio in favor of females, found in both migrants and wintering birds, may reflect a biased sex ratio in the population (Kjellén 1992).

Goshawk (*Accipiter gentilis*).—Most Goshawks breeding in Scandinavia are more or less resident. It is a comparatively sparse migrant at Falsterbo (Table 2). Banding recoveries show that northern breeders are more migratory than southern ones and that juveniles migrate furthest (Cramp et al. 1980). Since the Goshawk is a bird of the forest, only small numbers were recorded in semiopen habitats in Scania (Table 2). Juveniles prevailed among the migrants passing Falsterbo, as well as among the win-

tering birds in the semiopen habitats of Scania, and there was no significant difference in the age distribution between the two samples ($X^2 = 1.7$, $df = 1$, $P < 0.20$, $n = 213$).

In both Europe and North America, banding has shown that male Goshawks migrate further than females (Haukioja and Haukioja 1970, Mueller et al. 1977). This is supported by the counts at Falsterbo, where most migrating juveniles were males and all migrating adults were males (Table 2). In comparison, the sex ratio seems to be unbiased among the small sample of wintering birds.

Sparrowhawk (*Accipiter nisus*).—The Sparrowhawk is the most numerous migrant at Falsterbo in most years. It is also a fairly common wintering bird in southern Sweden, but due to its elusive habits is difficult to observe in large numbers (Table 2). In addition to the field observations of wintering birds given in Table 2, I inspected the collection of the Zoological Museum in Lund. It contained 32 Sparrowhawks found dead in Scania during the winter months: 3 adult males, 11 adult females, 8 juvenile males, and 10 juvenile females.

According to Newton (1979, 1986), males in Scotland winter primarily in forest, while females prefer more open habitats. This would probably result in more females occurring close to human settlements and, therefore, a greater chance of females being found. In the same way, juveniles are more likely to be found due to the greater risk of mortality close to human activities. These assumptions are supported by the higher proportion of males, as well as of adults, in the field observations of wintering birds compared to the museum specimens. Although birds in all four categories winter in Scania, the proportion of juveniles among wintering birds is lower than among the migrants at Falsterbo ($X^2 = 23$, $df = 1$, $P < 0.001$, $n = 4,572$).

Recoveries of Sparrowhawks banded in Denmark show that adults winter farther north than juveniles (Schelde 1960). Surprisingly, Finnish recoveries did not show any significant difference in winter range among ages and sexes (Saurola 1981). Recoveries of Sparrowhawks banded at Helgoland, Germany, and in eastern Europe show that old, as well as young, males on average migrate further than females of corresponding age (Belopolskij 1971, Cramp et al. 1980). The situation seems to be similar to that found in the closely related North American species, the Sharp-shinned Hawk (*Accipiter*

striatus), where females winter north of males and adults further north than juveniles (Clark 1985). However, other recoveries of the same species indicate that females (most likely mainly juveniles) winter south of males (Evans and Rosenfield 1985). No clear bias in the sex ratio can be seen in the small sample of wintering birds represented in Table 2.

Common Buzzard (Buteo buteo).—The proportion of juveniles at Falsterbo varied little in the four years apart from a higher percentage in 1988, most likely due to better breeding success (Table 1). There seems to be a correlation between the proportion of juveniles among the autumn migrants and among wintering birds the following winter. However, data cover only four years, and the correlation is not statistically significant ($r = 0.93$, $P = 0.07$, $n = 4$).

Most Scandinavian Common Buzzards are migratory and wintering occurs only in the southernmost part of Scandinavia. It is, however, the most numerous raptor in Scania in winter. From Table 1 it is evident that the proportion of juveniles is higher among migrants than wintering birds ($X^2 = 112$, $df = 1$, $P < 0.001$, $n = 15,147$). This indicates that adults, in northwestern Europe, generally winter north of juveniles. Recoveries of the most similar species in North America, the Red-tailed Hawk (*B. jamaicensis*), show that adults winter north of juveniles (Brinker and Erdman 1985).

Presumably, most buzzards wintering in Scania are of local origin. One way to investigate this is to look at the number of white-phase birds. These almost-white birds constitute a small but significant proportion of the breeding birds in Scania, but are very rare further north in Scandinavia (Ulfstrand 1977). Therefore, they can be assumed to represent a southern population. Of the aged Common Buzzards among the migrants in the autumns of 1990 and 1991, white birds constituted 2% of the adults ($n = 4,521$) and 6% of the juveniles ($n = 1,861$). This can be compared to 8% of adults ($n = 160$) and 10% of juveniles ($n = 42$) among birds wintering in Scania 1990/1991. The proportion of white birds, thus, was significantly higher among wintering birds than migrants ($X^2 = 17$, $df = 1$, $P < 0.001$, $n = 6,584$). These results support the idea that there is a larger proportion of birds from the southern population among the wintering buzzards, and also indicate that the juveniles in this population are more migratory than adults.

According to Sylvén (1978), Common Buzzards defend specific winter territories. Adults are presumably dominant over juveniles, forcing them to leave the breeding area in winter. The central part of Scania generally contains more forest and because of this more breeding territories of Common Buzzards than the coastal zone. In the winters of 1988/1989 and 1990/1991 the observed wintering buzzards were divided into two groups: those observed in coastal areas within approximately 15 km of the coastline; and those observed inland in the rest of Scania. Juveniles were significantly more common in the coastal group, comprising 36% of the observed birds but only 16% of the birds wintering inland ($X^2 = 17$, $df = 1$, $P < 0.001$, $n = 320$). This supports the idea that juveniles are driven away from the breeding areas and have to winter in peripheral areas of Scania or migrate south.

Rough-legged Hawk (Buteo lagopus).—The Rough-legged Hawk abandons its northern breeding grounds completely in winter. Most Fennoscandian breeders winter in central and eastern Europe (Cramp et al. 1980, Dobler et al. 1991). In the first two years, only adults and juveniles were separated, but after this adults were divided into adult males, adult females and second-year birds (second winter; Table 4).

Unlike the other species in this study, the Rough-legged Hawk had a significantly higher proportion of juveniles among wintering birds as compared to migrants at Falsterbo ($X^2 = 73$, $df = 1$, $P < 0.001$, $n = 3,259$). Since this species is more common on the Swedish eastern coast than other raptors, the difference could be due to a higher proportion of adults migrating southeast. To investigate this, the age composition of migrants at Falsterbo was compared with that at Ottenby on the island of Öland, in southeastern Sweden (Fig. 1). Regular observations and counts of migrating Rough-legged Hawks at Ottenby were conducted by personnel from Ottenby Bird Observatory in the autumns of 1989 and 1990. Since the proportion of juveniles was significantly higher at Ottenby (31%, $n = 1,352$) than at Falsterbo ($X^2 = 70$, $df = 1$, $P < 0.001$, $n = 2,175$), the higher percentage among wintering birds cannot be explained by different migration routes. It is likely that adult birds generally winter further south in Europe.

Winter movements have also been recorded; an influx to Baden-Württemberg, southwestern Germany in January 1987, being caused by ex-

TABLE 4. Numbers (percents in parentheses) of males, females, second-year birds and juveniles of Rough-legged Hawk among migrants at Falsterbo in autumn 1987–1990, and among birds wintering in Scania the following winter.

Year	Migrants					Wintering birds				
	Male	Female	Second-year	Juvenile	Total	Male	Female	Second-year	Juvenile	Total
1987	976* (66)	—	—	504 (34)	1,480	36* (32)	—	—	76 (68)	112
1988	606* (71)	—	—	246 (29)	852	43* (56)	—	—	34 (44)	77
1989	342 (36)	232 (24)	117 (12)	264 (28)	955	6 (13)	16 (34)	3 (6)	22 (47)	47
1990	427 (45)	380 (40)	82 (9)	58 (6)	947	22 (45)	18 (37)	2 (4)	7 (14)	49
Total	769 (40)	612 (32)	199 (10)	1,072 (25)	4,234	28 (29)	34 (35)	5 (5)	139 (49)	285

* Sexes and second-year birds among adults were not distinguished in first two years; for these years, total figures are given under males.

tensive snow cover and cold spells in central Europe (Dobler et al. 1991). Of 51 birds wintering in Baden-Württemberg, 22% were juveniles, compared to 68% of wintering birds in Scania the same winter (Table 4). This suggests that, in general, adults winter further south. Dobler et al. (1991) did not find any significant differences between adult and juvenile Rough-legged Hawks in directions taken or distances moved in an analysis of 72 recoveries of birds ringed in Scandinavia and recovered on the European continent during the winter months, although juveniles were distributed over a slightly larger total area. According to Palmer et al. (1988), there is a tendency for juveniles to migrate further south than adults in North America.

Recoveries from North America show that, generally, females winter north of males (Gauthreaux 1985). In my study, females constituted 51% of the adult wintering birds versus 39% among adult migrants, indicating that the situation may be similar in Europe. However, the difference is not statistically significant ($X^2 = 2.9$, $df = 1$, $P < 0.10$, $n = 628$).

As in Northern Harriers, breeding success in northern Scandinavia may vary considerably among years due to fluctuations in rodent numbers. The low number of juveniles in 1990 (Table 4) was probably the result of an unusually poor breeding season. This was matched by a low number of young birds the following winter. There seems to be a correlation between the percentage of juveniles among migrants in autumn and the percentage among wintering birds the following winter, although the relationship is not quite significant ($r = 0.94$, $P = 0.06$, $n = 4$). Since the number of excursions was fairly constant over the four winters, the higher number of Rough-legged Hawks seen in the first

two winters (Table 4) probably indicates a larger number of wintering birds in Scania in these winters. In studies of wintering raptors in Michigan, both Rough-legged Hawks and Northern Harriers occurred in higher densities in years with high rodent numbers (Craighead and Craighead 1956).

Eurasian Kestrel (*Falco tinnunculus*).—Adult males, adult females and juveniles were distinguished (Table 3). Most Scandinavian breeders are migrants, but smaller numbers winter in southern Sweden. According to Wallin et al. (1985), Swedish kestrels show a leap-frog pattern of migration, with northern breeders wintering farther to the south. The proportion of juveniles recorded was significantly higher among migrants at Falsterbo than among wintering birds ($X^2 = 183$, $df = 1$, $P < 0.001$, $n = 1,159$). This agrees with information in Cramp et al. (1980) suggesting that juveniles migrate the farthest south.

The percentage of juveniles at Falsterbo remained surprisingly constant over the years, while the corresponding proportion among wintering birds varied more (Table 3). The sex ratio of the adults at Falsterbo varied somewhat between different years, but was even over the whole sample (Table 3). However, among wintering kestrels in Scania, males clearly predominated, making up 60% of the adults. Hence, there was a significant difference in sex in the composition of the samples of migrating and wintering adults ($X^2 = 12$, $df = 1$, $P < 0.001$, $n = 385$). According to Newton (1979), males are more resident than females in some falcons. Males have been shown to winter north of females in Eurasian Kestrels and American Kestrels (*F. sparverius*; Gauthreaux 1985, Arnold 1991). Most wintering adults in Scania seem to stay close to their breeding territories. Dutch

studies have shown Eurasian Kestrels to be more markedly territorial in winters when rodent numbers are low (Cavé 1968).

GENERAL DISCUSSION

The observed differences in sex and age ratio between autumn migrants at Falsterbo and birds wintering in Scania are summarized in Table 5. A higher proportion of birds of a particular sex or age category (among wintering birds as compared to migrants) indicates that this group on average winters further north.

In raptors, the female is generally the larger sex and, according to the body-size hypothesis and Bergmann's rule, females should winter north of males. For four species (Northern Harrier, Goshawk, Sparrowhawk and Rough-legged Hawk), our study indeed shows a higher percentage of females among wintering birds, but the differences are not significant. Banding recoveries have shown females to winter north of males in all four species (Watson 1977, Haukioja and Haukioja 1970, Belopolskij 1971, Gauthreaux 1985), which suggests that the body-size hypothesis may be the most plausible explanation. All four show a much more pronounced sexual size dimorphism than the Eurasian Kestrel (Cramp et al. 1980), the only species in this study where males, on average, winter north of females. Newton (1979) has also applied Bergmann's rule to the wintering strategies of two species pairs of eagles in the genus *Aquila*: (1) Imperial Eagle (*A. heliaca*) and Steppe Eagle (*A. rapax*); and (2) Spotted Eagle (*A. clanga*) and Lesser Spotted Eagle (*A. pomarina*). In each species pair, the larger species generally winters north of the smaller one. Further support for this hypothesis is provided by the Snowy Owl (*Nyctea scandiaca*), where adult females generally winter farther to the north and juvenile males farthest south in North America (Kerlinger and Lein 1986).

According to the social-dominance hypothesis, stronger and more dominant individuals force subordinate birds out of suitable winter territories. In most passerines, older birds dominate juveniles and males dominate females. This leads to the expectation that old males are most likely to be resident and young females most likely to migrate (e.g. Smith and Nilsson 1987). Due to reversed sexual size dimorphism in raptors, females should be dominant over males and, consequently, females should be more

TABLE 5. Differences in sex and age ratio in raptors between autumn migrants at Falsterbo and birds wintering in Scania (southern Sweden).

Ages
More adults among wintering birds.—Red Kite*, White-tailed Eagle, Northern Harrier*, Goshawk, Sparrowhawk*, Common Buzzard*, Eurasian Kestrel*.
More juveniles among wintering birds.—Rough-legged Hawk*.
Sexes
More males among wintering birds.—Eurasian Kestrel*.
More females among wintering birds.—Northern Harrier, Goshawk, Sparrowhawk, Rough-legged Hawk.

*, $P < 0.05$.

common among the wintering birds. This is what we found for four out of five species (Table 5). This hypothesis also could explain the generally higher proportion of adults among wintering versus migrating raptors. In seven of eight species (Table 5), adults on average winter north of juveniles. In most of these species at least some adults winter close to the breeding grounds. Juveniles may be driven from their natal territory and then must either migrate south or settle in less optimal habitats closer to the breeding grounds. The latter approach appears to be used by Common Buzzards as a significantly higher proportion of juveniles occurred in the coastal region than inland. Goshawks, Sparrowhawks, Common Buzzards and Eurasian Kestrels all defend intraspecific winter territories, while Red Kites and Northern Harriers often spend the night in communal roosts and have overlapping hunting territories (Newton 1979). The Northern Harriers in Scania are south of their breeding range. Most Red Kites wintering in Scania also breed in the province; however, given that the majority gather in roosts of up to 200 birds, they must not winter in their breeding territories. It is possible that juveniles migrating ahead of adults at Falsterbo (Kjellén 1992) are driven from the breeding grounds before the adults depart for the winter roosts in late autumn.

An interesting exception is the Rough-legged Hawk, the only species in my study with significantly more juveniles among wintering birds than among migrants. As with the Northern Harrier, all individuals spending the winter in Scania are well to the south of their breeding range, with the majority migrating even further to winter in central and eastern Europe. Scania

and northwestern Europe may constitute a less-optimal wintering region than the main wintering area farther south. Juveniles may be more common here because there is less competition from adults for winter territories. Such competition is indicated by higher densities of wintering Rough-legged Hawks, as well as some other raptors in rodent years in Michigan (Craighead and Craighead 1956). I know of no other raptor where juveniles winter north of adults. However, in a passerine, the Dark-eyed Junco (*Junco hyemalis*) in North America, young females in particular (but also young males) winter north of adults of the same sex (Ketterson and Nolan 1979). In the American Goldfinch (*Carduelis tristis*), immature males on average winter further north than older males (Prescott and Middleton 1990).

The arrival-time hypothesis can usually be reconciled with social dominance. Dominant individuals wintering further north most likely gain the advantage of arriving early on the breeding grounds. The sex responsible for establishing the nesting territory ought to gain the most by wintering close to the breeding grounds. Since males generally establish the territory in raptors (Newton 1979), females wintering further north (as in most cases in Table 5) appear to contradict the hypothesis. However the hypothesis may explain why male Eurasian Kestrels winter north of females. Wallin et al. (1985) showed a significantly higher reproductive output for wintering nonmigratory kestrels compared to migrants in a population in southwestern Sweden. American Kestrels and sometimes Eurasian Kestrels are cavity nesters. It is generally believed that hole-nesting birds are less migratory since it is important to arrive early to secure a good nest hole (Haartman 1968, Alerstam and Högstedt 1981).

Character divergence probably explains differential preferences for winter habitats by the two sexes of the Sparrowhawk (Newton 1979) and American Kestrel (Koplin 1973). This hypothesis does not, however, explain why one sex winters north of the other unless the preferred habitats and food are geographically separated. Also, it probably cannot account for the observed differences between age categories.

Migration cost does not seem to be a good explanation for the observed differences in Table 5, since costs ought to be higher in juveniles. As for flight energetics, the fact that smaller birds use a smaller absolute amount of energy

when migrating favors longer migration in the smaller sex. This often is the case in raptors, but may equally well be the result of the smaller males being less tolerant of cold environments, or being inferior competitors with the larger dominant females. Thus, different hypotheses do not result in mutually exclusive predictions.

All of the raptors in my study can be categorized as short-distance migrants. Generally, the differences in wintering areas between birds of different age and sex classes seem to be less pronounced the further a species migrates. No such differences have been demonstrated among raptors that migrate to the tropics. Recoveries of European Ospreys (*Pandion haliaetus*) show that they winter in Africa, but Österlöv (1977) did not find any differences in wintering area between juveniles and adults.

To conclude, dominance relations seem to provide the best explanation for the observed differences in the proportion of ages and sexes among migrant versus wintering raptors in southern Sweden. Generally, juveniles are dominated by adults and males by females. The higher proportion of male Eurasian Kestrels among wintering birds is probably explained by the importance of early male arrival on the breeding territories of this species.

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