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Risto Tornberg · Mikko Mönkkönen
Maarit Pahkala

Changes in diet and morphology of Finnish goshawks from 1960s to 1990s

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Abstract We studied the morphology of the goshawk in northern Finland by measuring skin and skeletal characters of 258 museum specimens dated between 1961 and 1997. We predicted a decrease in the size of male goshawks from the 1960s because availability of their main prey, grouse, has decreased since then and grouse have been replaced in the diet by smaller prey during the breeding season. Based on the assumption that winter is the most critical period for females, we predicted that female size should have increased because their winter diet consisted of more and more mountain hare, which is a prey generally larger than grouse. Analyses revealed that male size has indeed decreased since the 1960s, while adult females have increased in size. Our data suggest that these morphological shifts were the result of selective pressures due to changes in diet. We also found changes in the (size-independent) shape of the hawks. Relative wing and tail lengths of adult hawks became longer between 1980 and 1990 compared with the 1960–1970 period, while relative juvenile wing and tail lengths tended to decrease. As a result of these morphological changes size dimorphism between the sexes increased from the 1960s to the 1990s.

Key words Goshawk · Grouse · Mountain hare · Morphology · Reversed sexual size dimorphism

Introduction

The goshawk (*Accipiter gentilis*) is widely distributed in the forested areas of the boreal zone and in parts of the deciduous zone of the Palearctic and Nearctic regions (Fischer 1980). In northern Europe goshawks feed largely on various grouse species but female goshawks also take adult mountain hares (*Lepus timidus*) (Sulkava 1964; Widen 1987; Tornberg and Sulkava 1991). These prey types are larger than the main prey species in central and western Europe, such as doves, corvids, thrushes and rabbits (Opdam et al. 1977; Goszcynski and Pilatowski 1986; Bezzel et al. 1997). The differences in diet may be related to size differences between northern (larger) and southern (smaller) races of the goshawk (Eck 1982; Fischer 1980).

Grouse populations have greatly decreased in Finland over recent decades (Lindén and Rajala 1981). Before 1980 average grouse densities were about 2 times higher than after 1980. This was also reflected in the diet of the goshawks during the breeding season. Other, often smaller, prey like ducks, corvids, doves and young hares have to some degree replaced the grouse in the diet and caused a decrease in average prey weight (Tornberg and Sulkava 1991). The new prey types may demand different hunting strategies by goshawks because flight performance of grouse, for example, differs considerably from that of passerine birds, and taking small prey selects for small size and agility among predatory birds (Pennycuick 1975).

Because males are almost solely responsible for hunting from the onset of breeding until the chicks fledge (Newton 1979), one might predict that (1) males should become smaller when their main prey items decrease in size and that (2) there should also be changes in the shape of the hawk when hunting strategies change. In many birds of prey, small males have been found to be more effective hunters at times when small prey types are most abundant (Storer 1966; Ydenberg and Forbes 1991; Hakkarainen and Korpimäki 1991, 1995; Hakkarainen et al. 1996). Hakkarainen and Korpimäki (1995) reported that in breeding Tengmalm's owls (*Aegolius funereus*), small males were more successful in producing young during low vole years when the diet consisted of shrews and small birds. Larger males did better during vole peak years when owls preyed mostly on larger field voles (*Microtus agrestis*). If the smaller males are indeed better at providing food to their offspring under the current food conditions, then this ought to be reflected directly in their offspring overall in relatively rapid mor-

R. Tornberg (✉) · M. Mönkkönen · M. Pahkala
Department of Biology, University of Oulu, POB 3000,
FIN-90401 Oulu, Finland
e-mail risto.tornberg@oulu.fi
Fax: +358-8-5531227

phological changes (Schluter and Smith 1986; Grant and Grant 1989).

Females do not take part in providing food for the chicks until the end of the nestling period (Sulkava 1964; Newton 1979). Adult females tend to stay in their breeding territories year round. For females, therefore, prey availability during winter might be the most important limiting factor. Following the decline in grouse females seem to have shifted their hunting strategies in the winter towards hares (Höglund 1964; Kenward et al. 1981; R. Tornberg and A. Colpaert, unpublished work). Prey of the size of an adult hare is outside of a male's reach. We therefore predict (3) an increase in female size, because hares on average are much larger than grouse.

Here we test these predictions by comparing the morphology of museum specimens from before and after 1980. We analyse males and females separately because of the differences in the diet and in the behaviour between the sexes. We also control for the age of the museum specimens, young or old, and cause of deaths, i.e. whether an individual had starved or died accidentally. The different causes of death can reveal potential selection pressures. If, for example, both starved young birds and young birds killed by accidents tend to be smaller than adults, we might conclude that there is selection for larger body size. The goshawk is one of the most size-dimorphic raptors (Storer 1966; Reynolds 1972; Newton 1979). If our prediction that the males have become smaller and females larger turns out to be supported by the data, it also means that the size difference between the sexes has increased over the study period. We discuss our results in the light of hypotheses suggested to account for the reversed size dimorphism in birds.

Materials and methods

Changes in grouse density and their proportion in the diet of the goshawk

Long-term monitoring of the goshawk's breeding biology in the Oulu region (65°00'N, 25°30'E) has already provided data on the composition of the diet (Tornberg and Sulkava 1991; Tornberg 1997; R. Tornberg, unpublished work). The Finnish Game and Fisheries Research Institute has monitored grouse densities in Finland since the 1960s using line transect and wildlife triangle counts (Lindén et al. 1996). We made use of these data for the Oulu region to obtain estimates of grouse densities between 1961 and 1997.

Morphometric measurements

A total of 258 goshawk specimens was available for the analysis in the collection of the Zoological Museum of the University of Oulu. This number includes both skin and skeletal specimens. The collection originates from northern Finland and covers the period between 1961 and 1997. For each skin the following measurements (to the nearest 1 mm) were taken: body length (from tip of bill to base of tail feathers), tail length, bill length, tarsus length and total length (from the of the longest rectrices to tip of bill). Wing length was measured from flattened and straightened wings and tail lengths from the root to the tips of central retrices.

We took the following measurements (to the nearest 0.01 mm with two decimals) from skeletal specimens:

1. Sternum length from tip of spina to median back edge of sternum sternum breadth (median)
2. Sternum height (maximum)
3. Coracoid length (maximum)
4. Femur length
5. Humerus length from proximal tip (caput humeri) to tip of trochlea,
6. Pelvis length (length of the sacrum)
7. Pelvis breadth as the distance between the lower (outer) edges of the acetabulum (see Bährmann 1974)

Skeletal specimens did not include the outer bones of the limbs because these bones were usually left with the skins.

Skeletal measurements were taken by one person only (M.P.) but altogether four persons were involved in taking skin measurements, which is why skin measurements contain an unknown proportion of variability. All the persons involved have, however, measured specimens of both sexes, all ages and from both periods. We therefore feel that there is no serious systematic error in our data from this cause.

All birds were classified according to plumage into juveniles (first and second year birds) and adults (after second year birds). We grouped all individuals according to cause of death into (1) starved and (2) accidentally killed birds (normal body condition), which includes both shot specimens and those that died in collisions. If the cause of death was not accurately determined when the specimen was found, we used body weight as an indication of the cause of death. Adult and juvenile males were considered starved or at risk of starvation if they weighed less than 700 g or 650 g, respectively. In females the corresponding limits were 1100 g for adults and 1000 g for juveniles. Birds in which the possible cause of starvation was injury were excluded from the analysis. Starvation as a cause of death in males, but not in females, has become more common between 1980–1990s than earlier ($\chi^2=14.2$, $P<0.001$).

Data analysis

Univariate differences between sexes and age classes were analysed by *t*-tests. Since several univariate comparisons were made we adjusted the probability level according to the number of tests made for a given hypothesis. For 14 characters tested we used a *P*-value of 0.0036 as the critical *P*-level.

We used the principal component analysis (PCA) to extract orthogonal morphological factors from the data. PCA was run for skeletal, and skin measurements of sexes separately. The original variables were log-transformed for the PCA.

To analyse the effects of age (adults vs. juveniles), cause of death (starved vs. accidentally killed) and time period (1961–1979 vs. 1980–1997) on morphology we used ANOVA models for PC scores. This was justified because variances did not differ between any of the groups of classifying variables. Because of the unbalanced structure of the data we used the procedure recommended by Stewart-Oaten (1995) for *k*-way unbalanced ANOVA. We started with type-III sum of squares, and constructed ANOVA models with all possible 2-way interactions between independent variables. Type-III sum of squares seemed most appropriate as we expected the effects of period to be different for adult and young and starved and accidentally killed individuals. If no interaction term was significant we tested for the main effects using type-II sum of squares.

We calculated the size dimorphism index according to Storer (1966)

$$DI=100(\text{-}x_{\text{females}}–\text{-}x_{\text{males}})/0.5(\text{-}x_{\text{females}}+\text{-}x_{\text{males}})$$

where $\text{-}x_{\text{males}}$ and $\text{-}x_{\text{females}}$ are the mean values for males and females, respectively. DI was calculated for wing and sternum lengths to allow comparisons with data from other regions.

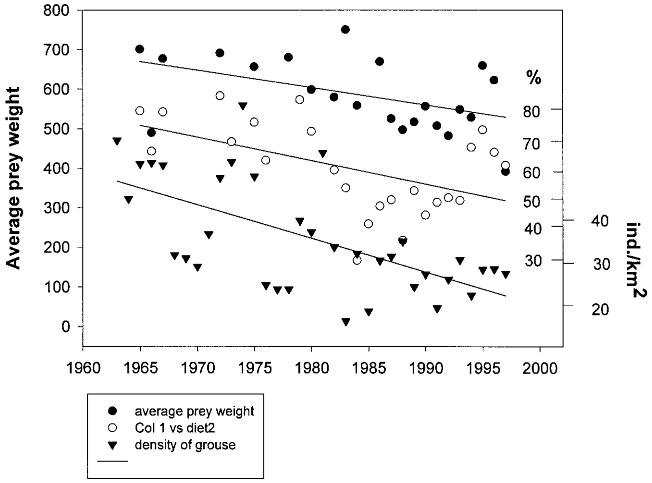

Fig. 1 The average weight of goshawks' prey in spring (*filled dots*), proportion of grouse in the diet of goshawks (*open dots*) and grouse density in Oulu region (*filled triangles*). Slope of regression for average prey weight $b=-4.41$, $F=6.05$, $P=0.023$, for grouse in diet $b=-5.96$, $F=7.93$, $P=0.01$ and for grouse density $b=-8.53$, $F=20.62$, $P<0.001$. Unpublished grouse density data were provided by Finnish game research institute

Results

Changes in goshawk diet and grouse density

Despite marked year-to-year fluctuations grouse densities show dramatic long-term decreases over the study period. Grouse numbers in the late 1990s were on average less than one-third of those in the early 1960s. Concomitantly, the percentage of grouse in the diet of the goshawk had also markedly decreased. Smaller prey groups like ducks, corvids, song birds, doves and young hares had to some degree replaced the grouse in the diet. This had resulted in a decrease on the average prey weight by some 20% from the 1960s to the 1990s (Fig. 1).

Univariate description

Averages of all skin and skeletal measurements for sexes and age classes are given in Table 1. Females were significantly larger than males in both age groups (all $P<0.0036$). There exist also certain differences between age groups within the sexes. Juvenile males tend to have longer tails than adults ($t=-5.933$, $df=108$, $P<0.001$, which is below the critical P-level of 0.0036), while in

Table 1 Skin and skeletal characters for sexes and age classes (CV% coefficient of variation)

Adults	Adult male				Adult female			
	Mean	SD	(*n*)	CV%	Mean	SD	(*n*)	CV%
Body length	280.0	12.0	(25)	4.3	316.8	13.8	(30)	4.4
Tail length	228.7	7.7	(26)	3.4	265.0	8.7	(31)	3.3
Wing length	330.3	6.8	(26)	2.1	372.3	7.0	(29)	1.9
Bill length	22.3	1.1	(25)	4.9	26.0	1.2	(28)	4.6
Tarsus length	79.5	3.6	(25)	4.5	89.1	3.7	(29)	4.2
Total length	548.1	16.2	(23)	3.0	628.7	14.5	(27)	2.3
Sternum length	82.5	3.1	(21)	3.8	91.2	2.7	(22)	3.0
Sternum breadth	39.1	1.0	(21)	2.6	45.2	2.1	(22)	4.7
Sternum height	21.2	0.7	(21)	3.2	22.9	1.1	(22)	4.6
Pelvis length	54.9	2.3	(19)	4.2	61.9	2.8	(23)	4.4
Pelvis breadth	30.0	1.0	(19)	3.5	34.5	1.6	(22)	4.5
Coracoid length	46.2	1.1	(18)	2.4	51.3	1.9	(19)	3.6
Humerus length	93.8	2.4	(19)	2.5	107.0	3.0	(19)	2.8
Femur length	77.7	2.1	(20)	2.7	88.1	2.4	(22)	2.7
Juveniles	Juvenile male				Juvenile female			
Body length	280.0	11.0	(80)	3.9	314.3	18.1	(85)	5.8
Tail length	238.7	7.1	(81)	3.0	268.0	5.9	(81)	2.2
Wing length	326.8	9.1	(79)	2.8	366.7	7.3	(86)	2.0
Bill length	22.0	1.2	(69)	5.5	25.3	1.6	(80)	6.3
Tarsus length	79.3	3.1	(78)	3.9	88.5	4.4	(83)	5.0
Total length	557.8	14.1	(69)	2.5	630.4	18.6	(75)	3.0
Sternum length	80.6	3.0	(67)	3.7	91.0	3.7	(72)	4.0
Sternum breadth	39.3	1.4	(67)	3.4	45.4	2.2	(72)	4.8
Sternum height	21.0	1.0	(65)	4.9	23.1	1.2	(72)	5.2
Pelvis length	53.8	2.0	(67)	3.7	61.7	2.4	(74)	3.9
Pelvis breadth	29.5	1.5	(67)	4.9	33.0	1.9	(74)	5.7
Coracoid length	45.2	1.6	(66)	3.5	51.3	1.6	(74)	3.1
Humerus length	92.7	2.2	(61)	2.4	106.3	2.3	(72)	2.2
Femur length	76.9	2.0	(66)	2.6	87.6	2.1	(73)	2.4

Table 2 Scores of skin and skeletal measurements on first two principal component axes (PCAs), and proportion of total variance explained. The sexes were analysed separately

	Males		Females	
	PCA1	PCA2	PCA1	PCA2
Skin characters				
Bill length	0.071	0.115	0.090	0.272
Tarsus length	0.130	0.434	0.358	0.616
Wing length	0.752	–0.324	0.668	–0.391
Tail length	0.578	–0.678	0.453	–0.647
Body length	0.730	0.559	0.774	0.440
Total length	0.903	0.180	0.897	–0.034
%Variance explained	37.8	18.5	36.5	20.3
Skeletal characters				
Sternum length	0.738	0.378	0.760	–0.065
Sternum breadth	0.347	0.475	0.607	0.171
Sternum height	0.587	0.293	0.319	0.766
Pelvis length	0.557	–0.572	0.606	–0.363
Pelvis breadth	0.718	0.323	0.463	0.443
Coracoid length	0.803	–0.276	0.842	–0.113
Humerus length	0.897	–0.132	0.920	–0.093
Femur length	0.871	–0.218	0.898	–0.114
%Variance explained	50.6	12.8	49.9	12.3

females adults had longer wings than juveniles (*t*=3.852, *df*=115, *P*<0.001). All other comparisons were non-significant (*P*>0.0036). The within-sex and within-age group variation in different measurements seems to be relatively constant as CV varies between 2 and 6% (Table 1).

Multivariate analysis

The first principal axis (PCA1), which explained between 37% and 51% of the variation in morphological data, seemed to be an indicator of overall size both in males and in females. This is because all original skin and skeletal characters had positive loadings on PCA1 (Table 2; see Ricklefs and Travis 1980; Wiklund 1996). The second component (PCA2) extracted from skin measurements appeared to be a gradient from individuals with long tails and wings relative to body length and tarsus length in the negative end to relatively short tailed and winged individuals in the positive end. This pattern was remarkably similar for males and females (Table 2). Because PCA1 was clearly a size gradient, PCA2 can be assumed to describe the shape of the individuals independent of size.

Males, which had large sterna and wide pelvises relative to pelvis and limb bone lengths, scored high on the PCA2 extracted from the skeletal data. The biological significance of this morphological gradient remains obscure. High sterna in particular characterized females scoring high on the PCA2 of skeletal measurements (Table 2).

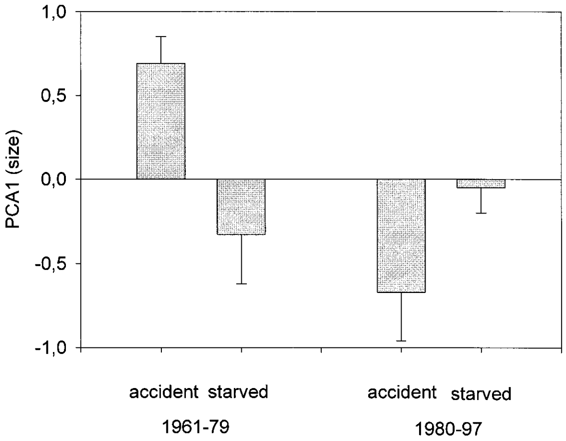

Fig. 2 Average PCA1 (size) scores of male goshawks for starved and normal birds for 1961–1979 (*period 1*) and 1980–1997 (*period 2*) based on skin characters. *Bars* indicate SEM

Table 3 ANOVA models for PCA1 and PCA2 scores in male skin characters. Because of significant interaction terms type-III sum of squares were used

	PCA1		
	F	*df*	*P*
Source of variation			
Period	5.45	1	0.02
Age	5.40	1	0.02
Cause of death	0.30	1	0.59
Period×age	0.45	1	0.50
Period×cause of death	4.44	1	0.04
Age×cause of death	0.40	1	0.53
Total model	6.12	6	<0.001
PCA2			
Period	0.79	1	0.38
Age	1.92	1	0.17
Cause of death	0.50	1	0.46
Period×age	3.87	1	0.05
Period×cause of death	0.02	1	0.90
Age×cause of death	2.05	1	0.16
Total model	2.46	6	0.03

Patterns in skin characters

In males there was a significant main effect of period, indicating that males were larger in 1961–1979 than in 1980–1997, as shown by the PCA1-scores. We also found that juvenile males were significantly larger than adults. No main effect for the cause of death was found. However, there was a significant interaction between the period and the cause of death. The size of accidentally killed birds was greater in 1961–1979 than in 1980–1997 whereas the opposite was true for starved birds (Fig. 2). Thus, small males tended to become starved during the period of 1960–1979 but larger ones in 1980–1997.

ANOVA for PCA2 scores suggests that there were significant differences in the shape of males between age groups but that these age differences were dependent on

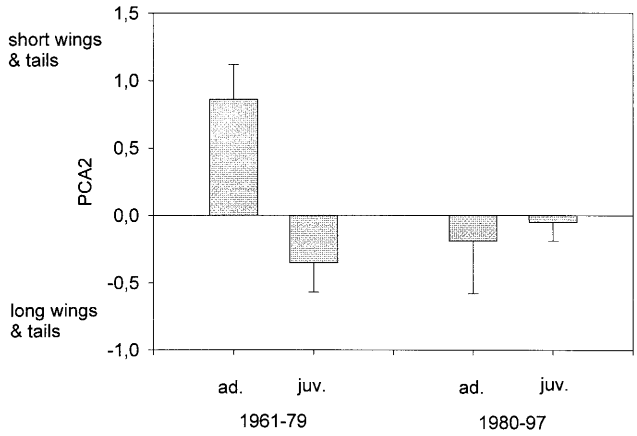

Fig. 3 Average PCA2 (body relationships) scores of male goshawks for adults and juveniles during the two periods based on skin characters. *Bars* indicate SEM

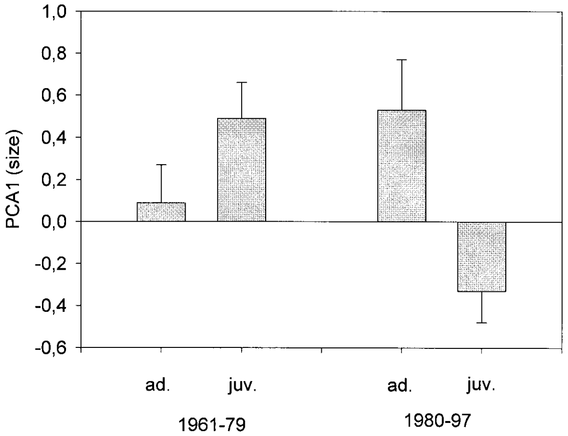

Fig. 4 Average PCA1 scores for adult and juvenile females during the two periods based on skin characters. *Bars* indicate SEM

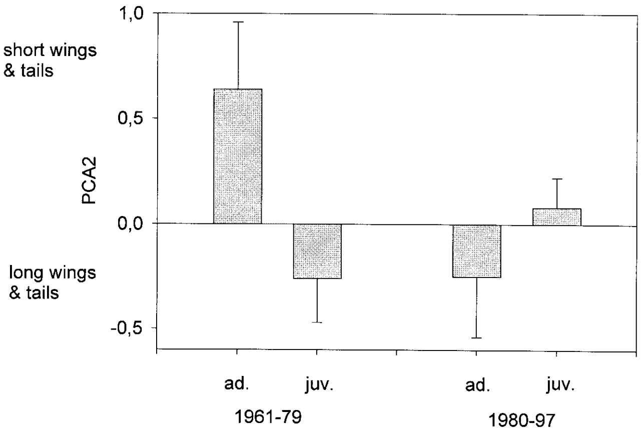

Fig. 5 Averages of PCA2 factor scores extracted from skin characters for adult and juvenile females during the two periods

Table 4 ANOVA models for PCA1 and PCA2 scores in female skin characters. Because of significant interaction terms type-III sum of squares were used

	PCA1		
	F	*df*	*P*
Source of variation			
Period	0.36	1	0.55
Age	0.78	1	0.38
Cause of death	2.65	1	0.11
Period×age	7.94	1	<0.01
Period×cause of death	0.38	1	0.54
Age×cause of death	1.25	1	0.27
Total model	2.46	6	<0.01
PCA2			
Period	0.99	1	0.32
Age	1.16	1	0.28
Cause of death	0.63	1	0.43
Period×age	6.14	1	0.02
Period×cause of death	0.41	1	0.52
Age×cause of death	0.47	1	0.50
Total model	1.41	6	0.22

the period (Table 3). In general, juvenile males tended to score lower on the PCA2 than adult males, which suggests that juveniles have relatively longer wings and tails. This pattern, however, was reversed during the 1980–1997 period. Adults had become relatively longer-winged and longer-tailed compared with males and juveniles before the 1980s (Fig. 3). In summary, the morphological changes among male goshawks have resulted in more “sparrowhawk-like” morphology during the 1980–1997 period than in 1961–1979.

We found a highly significant interaction effect between period and age on the PCA1-scores of the females (Table 4). Adult females became larger but juvenile females became smaller from the 1961–1979 period to the 1980–1997 period (Fig. 4). In 1961–1979 juveniles were larger than adults while in 1980–1997 adults were larger than juveniles.

The change in the females seems to parallel that of the males (Table 4). In the males, period and age on the PCA2-scores interacted strongly, but because of the total model’s limitations these results must be interpreted with caution. Thus, adult females seem to have been larger (Fig. 4) and to have had longer wings and tails during the period 1980–1997 as compared with 1961–1979 (Fig. 5). Quite the opposite patterns appear to apply to the juveniles.

Patterns in skeletal characters

No interaction terms were found to be significant in ANOVA models with type-III sum of squares in any of the analyses for PCA scores extracted from skeletal characters. We therefore fitted ANOVA-models with type-II sum of squares to test for the main effects. Age turned out to have a significant main effect on PCA1 scores in male goshawks (*F*=5.25, *df*=1, *P*=0.026) but the total

Table 5 Dimorphism indices of adults and juveniles in Northern Finland during 1961–1979 (period 1) and 1980–1997 (period 2), and in other parts of Europe and North America, calculated on the basis of sternum and wing lengths. Data for Sweden from Marcström and Kenward (1981), for Europe from Eck (1982) and for North America from Storer (1966)

	Period	Sternum	Wing
N. Finland ad.	1961–1979	7.38	11.4
	1980–1997	11.79	12.7
N. Finland juv.	1961–1979	12.20	11.0
	1980–1997	12.10	11.8
Sweden ad.		10.57	12.6
Sweden juv.		9.94	11.7
Denmark		10.90	
Eastern Germany		10.25	12.0
Northern Germany		9.25	
Western Germany		8.62	11.6
Romania ad.		8.98	
Romania juv.		10.46	
Romania (ad.+juv.)		9.96	11.7
North America		–	9.3

model was not significant (*F*=2.03, *df*=3, *P*=0.12). Considering bone characters it seems that juvenile males tended to be smaller than adult males. For females a marginally significant model was found for PCA1 scores (*F*=2.41, *df*=3, *P*=0.074). Starved females tended to be smaller than other females (main effect: *F*=3.05, *df*=1, *P*=0.085). No shape-related patterns (PCA2) were found to be significant.

Change in dimorphism

Because males were smaller and females were larger in 1980–1997 than in 1961–1979 it is obvious that size dimorphism has increased. To illustrate this further we calculated size dimorphism indices based on wing lengths and sternum lengths separately for the periods 1961–1979 and 1980–1997 (Table 5). These index values show that in both adults and juveniles wing length dimorphism had become more pronounced, but sternum length dimorphism increased only in adults. A comparison with estimates of size dimorphism from other regions based on the same measurements showed that the index values in northern Finland during 1980–1997 were not exceptionally high, but of the same magnitude as in Sweden and Central Europe. In contrast it seems that size dimorphism in northern Finland during 1960–1979 was lower than average.

Discussion

We found that males have become smaller and females larger in 1980–1997 compared with 1961–1979. These changes match well with the diet-related predictions we made and we can think of no other hypothesis that might explain the observed morphological changes. Rapid diet-related evolutionary changes have also been found in the song sparrows (*Melospiza melodia*) and in Darwin's finches (Schluter and Smith 1986; Grant and Grant 1989). These changes have not, however, remained constant.

Among males, starved individuals were smaller than those of normal body condition in 1961–1979 whereas in 1980–1997 starved individuals were larger than other males. This suggests that large size was selected for during 1961–1979 but small size was favoured by selection during 1980–1997. In the 1960s and 1970s, when there were more large grouse species available, larger males did better than small ones. At present, however, small males may be more able to replace grouse with smaller birds and mammals. The fact that starvation had become a more common cause of death in males, but not in females, over the study period implies that males suffer more from starvation than females under the present food conditions (see Kenward et al. 1991).

Among females size changes over time were age-related. Adult females became larger while juveniles diminished in size. This pattern can also be interpreted in terms of a reversal in selection pressure. If there had been directional selection for smaller size among females in 1961–1979, larger juveniles would have suffered disproportionately higher mortality than smaller juveniles, resulting in adults being smaller than juveniles in the museum data. By contrast, selection for larger female size in 1980–1997 has resulted in adults being larger than juveniles among females. Starved females were smaller than females of normal body condition, according to our skeletal data, suggesting selection for larger body size.

Large size may be beneficial for females in winter when they prey upon large prey such as mountain hares (*Lepus timidus*) (Kenward 1982; Widen 1987; R. Tornberg and A. Colbert, unpublished work; see also Ydenberg and Forbes 1991), the proportion of which has increased in the bird's winter diet. In North America the corresponding lagomorph species, the snow-shoe hare (*Lepus americana*), weighs only half as much as the mountain hare. Presumably as a consequence of this, female goshawks are smaller and size dimorphism between the sexes is less pronounced in North America than in Europe (Storer 1966; Kenward 1996).

During 1961–1979 adult goshawks had relatively short wings and tails compared with adults from 1980–1997. Goshawks use surprise attacks (Kenward 1982; Pennycuick et al. 1994), but often also chase grouse for some time using "power flight". Short wings may be better suited to power flight because short wings require less power in flapping flight (Mueller et al. 1981; Fox 1996). The smaller, longer-winged and longer-tailed male type of the 1980–1990s may be more suited to hunting of more agile prey types such as passerines, ducks, and waders, all of which have increased their proportions in the goshawk's diet during the breeding season (Tornberg and Sulkava 1991; Tornberg 1997). Goshawks hunting these kinds of prey require higher manoeuvrability, and the latter increases with decreasing body size (Andersson and Norberg 1981).

The morphological changes were more pronounced in skin than in skeletal characters. We have no convincing explanation for this, but perhaps skin characters are evolutionarily more flexible traits than bone dimensions. Also, if selection favours certain morphotypes, adjustments in the length of the feathers might be a more efficient response to these pressures than changes in bone dimensions. Furthermore there was an interesting contrast between skin and skeletal data. Juvenile males tended to be larger than adults in skin characters but smaller than adults in skeletal characters. This suggests contrasting relative size patterns between outer (skin) and inner (skeletal) body dimensions in juveniles and adults. The reason for this pattern remains open.

Sexual dimorphism increased from the 1960s as a consequence of opposite morphological trends in size, which were particularly pronounced in adult goshawks. Several hypotheses have attempted to explain the reversed size dimorphism (RSD) in birds. Because many hypotheses make similar or non-exclusive predictions about the changes in the level of dimorphism as a consequence of changes in prey availability, our data can not be used as a test between them.

The "small male hypothesis" states that selection favours small males because small males are assumed to be more efficient hunters than larger males during the early breeding season. This would result in RSD (Storer 1966; Reynolds 1972; Newton 1979; Hakkarainen and Korpimäki 1991; Ydenberg and Forbes 1991; Paton et al. 1994; Hakkarainen et al. 1996). Our data support this explanation for RSD, as goshawk males became smaller when their average prey decreased in size. The "starvation hypothesis" predicts larger female size when food supply becomes more unpredictable (Lundberg 1986; Korpimäki 1986). We do not know whether food supply for females has become more unpredictable or not, but hare populations certainly show wide fluctuations between years (Lindén et al. 1996). The "competition hypothesis" predicts greater segregation between the sexes when the resources decrease (MacArthur and Lewins 1967). Our results support also this hypothesis.

To summarize, male size has decreased markedly since the 1960s. We propose that the decrease of grouse abundance has resulted in a shift to smaller and possibly more agile prey types, which has favoured small, long-winged and long-tailed types. The selection for such types may be most intense during the nestling period when the male provides food for the whole family and prey size is at its lowest. The size of the females may be more affected by the size of the prey in their winter diet, which contains more and more large prey like mountain hare. In the summer, females do not hunt until late in the fledging period. Large size may also be useful for females while protecting the chicks, as the "big mother" hypotheses predict (see Mueller and Meyer 1985). Although the most plausible explanation for the patterns described here is the change in the availability of prey species, our data provide only correlative evidence. A study comparing the breeding success and winter survival between goshawks of different sizes would provide a direct test for the proposed causation.

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