A COMPARISON OF PREY SELECTION IN SYMPATRIC HARRIERS, *CIRCUS*, IN WESTERN EUROPE

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CONTENTS.

1. INTRODUCTION.

1.1. Aim of the study.

The present paper is a part of a comparative study of ecological and ethological differences in three sympatric species of harriers, Marsh Harrier (*Circus aeruginosus*, in this paper abbreviated to *C.a.*), Hen Harrier (*Circus cyaneus*, abbreviated to *C.c.*) and Montagu's Harrier (*Circus pygargus*, abbreviated to *C.p.*), in Western Europe. The species are relatively closely related and until now their ecology has been considered to be rather similar.

Species with the same ecological requirements cannot persist next to each other under the same circumstances, and competition will ultimately lead to the exclusion of all but one of them. This postulate is often referred to as the the Gausian principle, although authors use various choice of words in stating the hypothesis; see discussions in HARDIN (1960), MAYR (1963), LACK (1966) and YAPP (1970).

Competition can be defined as a situation where two rivals cause prejudice to each other because they seek simultaneously an essential resource of the environment. In non-specialized species like harriers interspecific competition for a restricted number of objects may occur without severe disadvantage to the birds. The quality and quantity of the objects of competition will be decisive of whether exclusion of competing species will eventually be realized. Apparently the three species of harriers are able to persist side by side in the same breeding area, so that under that circumstance their interspecific relations can be described as follows:

(*a*) The ecological requirements of all three species are present.

(*b*) Possible interspecific competition is restricted to less important objects.

(*c*) Other common sources are very abundant, so that competition does not occur (LACK, 1946 and 1966) or they are exploited by each species in different specific ways, so that competition becomes restricted to a limited number of occasions.

Changing circumstances however might enlarge competition, when in spite of the fact that the ecological requirements of the species are present, competition is forced to more important objects, e.g. when particular food sources are restricted in number or extent.

As specific ways of ecological differentiation of related species are prerequisites for dispersal and speciation, our harrier studies have been focused on the ecological relationships of the three species. In this paper interspecific and intraspecific differences in food requirement and factors related to prey selection will be considered. Publications dealing with other ecological requirements are in preparation and will consider hunting habits and breeding biology.

Ecological properties are closely related to morphological and structural characters. The latter have been studied in harriers by NIEBOER (1973). Some of the ecological data collected in the course of our harrier study are referred to by NIEBOER and myself, though our conclusions will not necessarily concur.

1.2. Acknowledgements.

The study has been achieved under the supervision of Prof. Dr. K.H. VOOUS, to whom I acknowledge my indebtness for his genial and stimulating attention to my work. I am owing gratitude to Dr. E. NIEBOER, Dr. T. DE VRIES, and P. OPDAM for many useful discussions, to R. MURRAY who read and corrected the English text of this paper, to Dr. L. HOFFMANN who very kindly granted hospitality in the biological station «La Tour du Valat» in the Camargue, in 1969 and 1970, to his assistents H. KOWALSKI, H. HAFNER, A. JOHNSON, J. WALMSLAY and O. BEBER for their help and for the very hearty way they took my wife and myself into their walks of life, to Dr. J. BLONDEL for criticizing the working up of some data, to Dr. P. HEURTEAUX for meteorological and geographical data of the Camargue, to L. KÉRAUTRET who introduced me to the study area in Northern France, to the Staatsbosbeheer in Limburg, Ameland and Terschelling for kindly allowing access to their districts, to M.H. VAN DEURSEN in Groote Peel and H.J. TIMMER in Ameland for the hearty cooperation, to J.C. TANIS and W. DUBBELDAM for criticizing prey density data in Ameland and Terschelling, to the Rijksdienst voor de IJsselmeerpolders for their licences to conduct investigation in Flevoland and for other valuable assistance, particularly through Drs. H. de Jong, to Dr. J. Wattel and C. Roogselaar (Zoological Museum, Amsterdam) and E. Osieck for very obliging help in identifying pellet contents and prey remnants. I am grateful to G.W.H. van den Berg, who prepared the illustrations in this study, and to Dr. J. Jager for his statistical advices.

My thanks to all of the students mentioned in Chapter 4.1. who collected data and provided discussion and criticism which have been of very great value.

The study was made possible by the financial support of the Rijksinstituut voor Natuurbehoud (for studies in Ameland, Terschelling, Groote Peel) and grants by the Nederlandse Organisatie voor Zuiver Wetenschappelijk Onderzoek (all other study areas). The Biological Laboratory of the Vrije Universiteit in Amsterdam granted hospitality and other facilities for the study.

Throughout the whole study period from 1969 onwards my wife assisted me with observations in the field, with the collation of the data, by criticism, through discussion and also by her warm encouragement.

2. SPECIES STUDIED.

2.1. Morphology.

The morphology of harriers has been thoroughly studied by Nieboer (1973). Some general and striking morphological and structural characters will be referred to.

Like the other harriers, the three species studied are long-winged, long-tailed and long-legged birds of prey, living in open country. The three species all nest on the ground. The sexual dimorphism is exceptional among birds of prey, as the sexes show differences in both structure and plumage.

There is a tendency for the larger harriers to have a smaller flight apparatus in relation to body weight and a relatively larger prey catching apparatus (tarsus, sum of toes, sum of claws, and bill). In relation to body weight *C.p.* has the longest tail, *C.a.* the shortest. However in relation to wing length (wrist to tip) *C.c.* has the longest tail.

According to Brown and Amadon (1968) the wing loading is highest in *C a.*, lowest in *C.p.* The wing measurements and structure of *C.p.* are considered to be advantageous for long distance flights in less favourable weather, e.g. during migration (Nieboer, 1973).

2.2. Distribution.

Data have been taken from Voous (1960), Dementiev (1951) and Nieboer (1973). See Table 1.

All species concerned occur in boreal, temperate, Mediterranean, steppe and desert zones and overlap widely in the Palaearctic region. *C.c.* has the most extensive distribution, in the Eastern Palaearctic and the Nearctic. The range of *C.p.* is least extensive of all as it does not reach Eastern Asia.

Table 1: Distribution data.

Species	Distribution (breeding range)	Limits in Palaearctic nearest July isotherm		Winter range of palaearctic birds
		northern	southern	
C.a.	Palaearctic	60° F	80° F	temperate to tropical
C.c.	Holarctic and South America	50°-53° F	75° F	temperate and Mediterranean
C.p.	Palaearctic	62° F	78° F	mainly tropical

3. METHODS.

3.1. Choice of study areas.

For the present study those places were selected where two or three species nest together in varying densities (Ameland, Terschelling, Flevoland, Northern France). Here the harriers have to select their prey from the same prey spectrum under comparable circumstances. To achieve this purpose many breeding seasons were spent by students in Ameland and Terschelling. Information from the mainland was also considered to be indispensable as the limited variation in prey supply, the small dimensions and the morphology of the islands possibly influence the general behaviour of the harriers. In addition numbers of *C.a.* were very low in the islands. Therefore *C.a.* was also studied in Southern France, where it was found to nest not far from *C.p.* Unfortunately in some areas the breeding success of one or more species did not come up to expectations (Groote Peel, Northern France).

3.2. Collection of food data.

3.2.1. *Nest observations.*

Nest observations were made from a well camouflaged hide of 1 × 1 × 1 m, placed near a nest with young at distances varying from 2—12 m. In *C.c.* and *C.p.* the distance to the nest was generally not closer than 5 m, but incidentally the structure of the vegetation dictated a closer distance. In *C.a.*, which as a rule is warier, a distance of at least 8 m was maintained. Dependent on the suspected shyness of the adults the hide was moved toward its final position on successive days in one to three steps. The interior of the hide had to be kept as dark as possible to make the observer invisible from outside. In particular, *C.a.* used to gaze very keenly through the hide peep-hole, which had to be kept as narrow as possible.

Going to and leaving the hide the observer was always accompanied by a second person.

When observing in the hide an imminent feeding of the young was often heralded by the male calling the female on his approach with prey, and when passing the prey females and males usually called loudly. But this could not always be relied upon as some parent birds were very silent or else the prey was passed at a considerable distance from the nest site. As a consequence, under these circumstances the help of a second field observer nearby was often necessary to ascertain which of the parent birds was supplying the food.

3.2.2. *Prey remnants from nest and field.*

Prey remnants were found on and near the nests. Breeding females of *C.a.* and *C.p.* often chose fixed stations in the vicinity of their nests to consume the prey supplied by the male. On these plucking posts remmants of prey that had been fed to the young could also be collected. These posts mostly were bundles of flattened marsh vegetation or a small elevation in the terrain.

Prey remnants were identified by direct comparison with material in the collection of the Zoological Museum of Amsterdam, by consulting descriptions and pictures in LOCHTE (1938) and by using the identification tables and descriptions in DAY (1966).

3.2.3. *Pellets from nests, field and roosting sites.*

Pellets of young were collected at the nests. Pellets of adults were collected at their regular perches, at plucking stations near the nests (see 3.2.2.) and, in winter, at their communal roosts.

Identification of remnants was made in the same way as for the prey remnants. In the presentation of the data no more than one individual of a prey species was credited to any one pellet. This was done because FITCH et al. (in Luttich et al., 1970) found that on the average each pellet occurrence corresponded to one individual prey item, and also for practical reasons.

3.2.4. *Other field observations.*

These include all observations of birds capturing and carrying prey, and passing prey from the male to the female during the breeding period. Whenever possible the size of the prey was estimated and noted, but recognition of the prey was generally impossible, except in the case of snakes and eels. Also, the sex of the harrier and the habitat in which the capture had taken place were noted.

3.3. Weather data.

Weather data were obtained from the Koninklijk Nederlands Meteorologisch Instituut (KNMI), from the Station Biologique de la Tour du Valat and from our own measurements. Since no wind velocity data was available from Ameland and Terschelling data from Vlieland was used.

4. DESCRIPTION OF STUDY AREAS AND OBSERVATION PERIODS.

The study areas, years and students are summarized in Tables 2 and 3 and Figure 1. The habitats and fauna of each of the study areas will be briefly discussed, with particular reference to the density of prey species in each distinct habitat. Most of the prey density data (Table 4) are estimates, as time was seldom available for more detailed census work. For estimates of prey densities in Terschelling data from Tanis (1963) and Bijleveld (1959) were used; in Groote Peel prey population densities were derived from counts by M.H.v. Deursen and the author; for a bird census in Northern France see Schipper (1971); for Southern France see Hoffmann (1958) and von Fritsch (1965, 1968). Critical comments on density data were kindly supplied by B.A.P.J. Daemen, T.P.J. Loorij and J.v. Dijk (for Ameland),

Table 2: Food studies made during the breeding season.

Locality	Year	Species studied			Students
		C.p.	*C.c.*	*C.a.*	
Ameland	1964	+	+	+	R. Bekius
	1967	+	+		C. v.d. Kraan, N.J. v. Strien
	1970	+	+		B.A.P.J. Daemen, T.P.J. Loorij
Terschelling	1959	+	+	+	E. Nieboer, J. v.d. Toorn
	1961	+	+		T. v. Dijk, T. de Vries
	1962	+	+		J.J. Geuze, P.H. Nienhuis
	1968	+	+		G. Boere, M. Cheng, F. Feldmann K. Velt
Flevoland	1971	+	+	+	W. Schipper
	1972		+		W. Schipper, S. Wiersema
Groote Peel	1965	+		+	J.H. Ietswaart, W. Schipper
Northern France	1970	+	+	+	W. Schipper
Southern France	1969	+		+	W. Schipper

Table 3: Food studies made in winter.

Locality	Year	Species studied		Students
		C.c.	*C.a.*	
Terschelling	1969/70	+		G. Boere, W. Schipper
Lauwerspolder	1970/71	+		L. Buurma
Flevoland	1969/70	+		W. Schipper
	1970/71	+		L. Buurma
Southern France	1970/71		+	W. Schipper

J.J.C. TANIS and W. DUBBELDAM (for Terschelling), M.H.v. DEURSEN (for Groote Peel) and J. BLONDEL, H. HAFFNER and H. KOWALSKI (for Southern France).

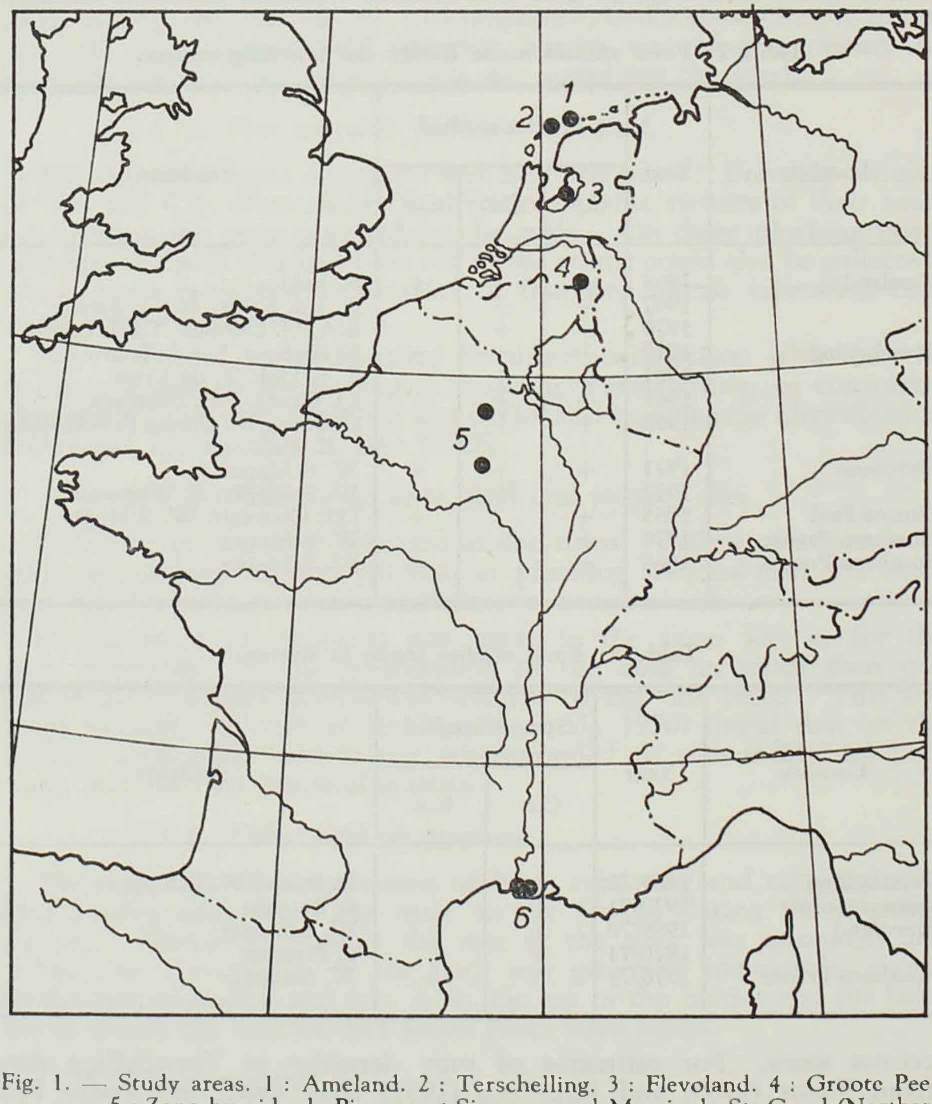

Fig. 1. — Study areas. 1 : Ameland. 2 : Terschelling. 3 : Flevoland. 4 : Groote Peel. 5 : Zone humide de Pierrepont-Sissonne and Marais de St- Gond (Northern France). 6 : Camargue and Crau (Southern France).

4.1. Netherlands.

4.1.1. *Ameland.*

The island of Ameland is largely composed of two distinct areas:

a. Dunes (1800 acres) along the North Sea coast; the following habitats were distinguished:

Land dunes– more inland dunes and dikes, covered with *Ammophila arenaria* and other grasses, occasionally with a scanty vegetation of *Salix repens* and *Hippophaë rhamnoides;*

sea dunes– coastal, growing sand dunes with an open vegetation of *Ammophila arenaria*;

moist valleys– dune valleys with a low vegetation containing among others *Schoenus nigricans, Salix repens, Hippophaë rhamnoides* and other small shrubs;

dry valleys– dune valleys covered with a thorny scrub of *Hippophaë rhamnoides* and *Salix repens*;

reed marshes– reedbeds with old and fresh *Phragmites communis* and small patches of open water.

b. Cultivated areas (2600 acres), including grasslands. Other habitats, like conifer plantations will not be considered here, as they were of no importance to harriers.

The harriers nested in the dunes and hunted over dunes and cultivated land.

Of the distinct prey categories, lizards were not present in Ameland (present in Terschelling) but voles (*Microtus arvalis*) occurred (not present in Terschelling). Pheasants appeared to be more numerous in Ameland. Amongst the larger mammals rabbits were especially numerous.

4.1.2. *Terschelling.*

The island Terschelling, situated west of Ameland, is largely composed of three distinct areas (Tanis, 1963):

(*a*) Dunes (3200 acres): habitats as in Ameland.

(*b*) Cultivated areas (1800 acres) in the southern part along the Waddensea. In this part some duck decoys are situated.

(c) Boschplaat (1700 acres, Groede included), a vast plain in the eastern part of the island with a low salt vegetation, intersected by salt-water creeks. Some low sand dunes are present (see a).

All harrier studies were carried out on the eastern part of the island, where the harriers nested in the dunes, and hunted in the dunes, the grasslands in the south and the Boschplaat.

Table 4: Estimates of average prey densities (specimens per 1 000 acres habita surface) in May, June and July. Unless specified young and adults ar included.

Legend :
\+ 10- 100 specimens;
\++ 100- 1 000 specimens;
\+++ 1 000-10 000 specimens;
\++++ more than 10 000.

In Southern France one should attribute relative values only to these symb

	Ameland					
	land dunes	moist dune valleys	dry dune valleys	reed marshes	sea dunes	cultivated
Large insects (*)						
Fish, frogs		++		+++		+
Snakes						
Lizards						
Anatidae, Rallidae, non breeding Limicolae, *Larus ridibundus*,	++	+++	++	++	+	+++
Other Limicolae, Phasianidae	+++	++	+++		++	+++
Passeriformes	+++	++	+++	+++	++	++
Small mammals (*)	++	+	+++			+++
Larger mammals (*)	+++	+	++		++	+

	Gr. Peel		N. France		Southe	
					La T	
	moors and marshy land	meadows and crops	marshy land	crops	Salicornietum fruticosae	Sealavender
Large insects	++	++	++		+	+++
Fish, frogs	++	+	+++			
Snakes	+		+			+++
Lizards	+++	+	++			+++
Anatidae, Rallidae, non breeding Limicolae, *Larus ridibundus*,	+++	++	+++		+	
Other Limicolae, Phasianidae	++	+++	+	+		
Passeriformes	+++	+++	+++	+++	+	++
Small mammals	+++	+++	++	++		+++
Larger mammals	++	++	+			+++

rce, common, numerous, and very numerous, respectively

Terschelling							Flevoland		
and duck decoys	moist dune valleys	dry dune valleys	reed marshes	sea dunes	cultivated area	Boschplaat, Groede, without dunes	reed marshes	crops	verges (roads, dikes, etc.)
									++
	++		+++		+		+		
++		+++		+					
+	+++	++	++	+	+++	+++	+++	+	++
+	++	++		++	+++	+++	+++	+++	+++
++	++(+)	+++	+++	++	++	++	+++	+++	+++
+		++		+(+)		++(+)	+++	+++	+++
++	+	++		++	+	+	+++	+++	+++

nce

Valat and environs					La Crau		
Scirpus marshes	reed marshes	dry agricultural land	rice fields	edges with shrubs	marshy land	agricultural land, edges included	stony plain
+	+	++	+++	++++	+++	+++	+++
+++	++(+)		+		+++		
+(+)	++(+)	+	++	++++	++	++	++
		++		+++		++	++
++	+++		++		+++		
	++	++	+	++++	++	+++	+++
	+	++	+	+++	+	+++	++
	++	++	+	+++	+	++	+

(*) See Appendices 1-8.

Table 4 : Estimates of average prey densities (specimens per 1 000 acres habitat surface) in May, June and July. Unless specified young and adults are included.

Legend :
\+ 10- 100 specimens;
\+ + 100- 1 000 specimens;
\+ + + 1 000-10 000 specimens;
\+ + + + more than 10 000.

In Southern France one should attribute relative values only to these symbols :

	Ameland					
	land dunes	moist dune valleys	dry dune valleys	reed marshes	sea dunes	cultivated area
Large insects (*)						
Fish, frogs		++		+++		+
Snakes						
Lizards						
Anatidae, Rallidae, non breeding Limicolae, *Larus ridibundus*,	++	+++	++	++	+	+++
Other Limicolae, Phasianidae	+++	++	+++		++	+++
Passeriformes	+++	++	+++	+++	++	++
Small mammals (*)	++	+	+++			+++
Larger mammals (*)	+++	+	++		++	+

	Gr. Peel		N. France		Southern	
					La Tour	
	moors and marshy land	meadows and crops	marshy land	crops	Salicornietum fruticosae	Sealavender sward
Large insects	++	++	++		+	+++
Fish, frogs	++	+	+++			
Snakes	+		+			+++
Lizards	+++	+	++			+++
Anatidae, Rallidae, non breeding Limicolae, *Larus ridibundus*,	+++	++	+++		+	
Other Limicolae, Phasianidae	++	+++	+	+		
Passeriformes	+++	+++	+++	+++	+	++
Small mammals	+++	+++	++	++		+++
Larger mammals	++	++	+			+++

Scarce, common, numerous, and very numerous, respectively

Terschelling							Flevoland		
land dunes and duck decoys	moist dune valleys	dry dune valleys	reed marshes	sea dunes	cultivated area	Boschplaat, Groede, without dunes	reed marshes	crops	verges (roads, dikes, etc.)
									++
	++		+++		+		+		
+++		+++		+					
++	+++	++	++	+	+++	+++	+++	+	++
++	++	++		++	+++	++	+++	+++	+++
+++	++(+)	+++	+++	++	++	++	+++	+++	+++
++		++		+(+)		++(+)	+++	+++	+++
+++	+	++		++	+	+	+++	+++	+++

France

du Valat and environs					La Crau		
Scirpus marshes	reed marshes	dry agricultural land	rice fields	edges with shrubs	marshy land	agricultural land, edges included	stony plain
++	+	++	+++	++++	+++	+++	+++
++++	++(+)		+		+++		
++(+)	++(+)	+	++	++++	++	++	++
		++		+++		++	++
+++	+++		++		+++		
+	++	++	+	++++	++	+++	+++
+	+	++	+	+++	+	+++	++
+	++	++	+	+++	+	++	+

(*) See Appendices 1-8.

The prey species present resembled those of Ameland, with some notable differences, mentioned under ‚Ameland'. Of the small mammals *Apodemus sylvaticus* was the most common species; rabbits were numerous, as in Ameland.

For details concerning the avifauna see TANIS (1963).

4.1.3. *Flevoland and Lauwerspolder.*

The reclaimed areas of Flevoland are composed of two parts:

Oostelijk Flevoland (54000 acres), drained in 1957;

Zuidelijk Flevoland (43000 acres, drained in 1968.

After the reclamation of each of these areas, reed (*Phragmites communis*) was sown, and a gradual development undertaken by the state. In 1971 the main part of Oostelijk Flevoland had been leased to farmers and only the western third was still managed by the state. Here some reedbeds remained, including a rather large area of about 190 acres, where three sandy plains are found. Our field studies were mainly performed in and around this large reedbed, and in the adjoining parts of Zuidelijk Flevoland.

In 1971 a large part of Zuidelijk Flevoland was cultivated. The remaining areas still consisted of vast reedbeds of *Phragmites communis* and *Typha angustifolia*, here and there with large or small shallow pools. Locally willow shrub appeared. At the borders of the pools communities of *Senecio congestus* developed.

Most important agricultural crops in the state-managed cultivated area were cole seed, wheat, barley and flax.

Harriers bred chiefly in the reedbeds and hunted over the reedbeds and crops.

Although fish were locally abundant in the canals, this habitat was not considered as it did not appear to be of importance to any of the harrier species. Of the other prey categories pheasants and rabbits were very abundant. In 1972 the density of pheasants appeared to be higher than in 1971. Voles (*Microtus arvalis*) were numerous in 1971, but scarce in 1972.

For more details concerning the avifauna see CAVÉ (1961) and VAN ELBURG (1969).

At the time that pellets were collected in winter, numerous ducks, rails, pheasants and songbirds inhabited the reed marshes and wetlands. In this habitat *Micromys minutus* was also common. In the barren agricultural plains of Oostelijk Flevoland, voles (*Microtus arvalis*) were abundant in winter 1969/70, but less numerous in winter 1970/71. In this habitat wandering groups of songbirds were present.

Some pellets were collected in the Lauwerspolder, a recently reclaimed area near the Dutch Waddensea, in winter 1970/71. The density of *Microtus arvalis* was high, and flocks of songbirds were present.

4.1.4. *Groote Peel.*

The Groote Peel is a small remnant of about 1000 acres, of the vast area of moors and marshes that once covered part of the south of the Netherlands. Most of these areas have been cultivated and as a result the Groote Peel is now surrounded by meadows and agricultural land.

The Groote Peel itself is composed of sendy riolges with a vegetation dominated by *Calluna vulgaris*, alternated by large peat-bogs, where *Molinia caerulea* forms the most notable vegetation.

In many places oligotrophic lakes and pools have arisen, caused by peat-exploitation. In addition there is one rather large eutrophic lake, with reeds and shrub. Locally in the moors and peat-bogs small trees were present, particularly birch.

Harriers were breeding in the Groote Peel and hunted over the area and its surroundings. The densities of several prey species were not very high, but some categories, notably Anatidae, *Larus ridibundus* and Passeriformes were well represented.

4.2. France.

4.2.1. *Northern France*

Harriers were studied in two distinct areas:

(*a*) ,*Zone humide de Pierrepont-Sissonne*' (4600 acres);

(*b*) ,*Marais de St-Gond*' (4000 acres).

Both are rather broken up marshy areas, the former situated along the canalized river Souche, the latter, slightly drier, along the equally canalized river Petit Morin. Both marshes are enclosed by sloped or hilly agricultural land.

The *Zone humide de Pierrepont-Sissonne* consists of several wooded regions leaving open areas covered by a marsh vegetation of *Phragmites communis, Thypha angustifolia* and *Cladium mariscus*. For more details about the vegetation see FROMENT (1953). Locally fish-ponds have been excavated.

In the *Marais de St-Gond* fewer woods and fish-ponds are found. A scattered shrub vegetation was present in the reedbeds of both areas.

In Table 4 estimates of prey densities in the *Zone humide de Pierrepont-Sissonne* are given. They are probably comparable to those in the *Marais de St-Gond*. The numbers of larger mammals, especially rabbits, and young pheasants, were very low. Young Anatidae and small mammals (voles, mice) were not numerous. Conversely the density of *Rallus aquaticus* and *Gallinula chloropus* was high.

4.2.2. *Southern France.*

C.a. has been studied at the biological station ,La Tour du Valat' and its immediate surroundings in the Camargue; *C.p.* has been studied east of the Grand Rhône, near and in the plains of La Crau. A description of the habitats in these areas is found in Hoffman (1958) and von Frisch (1965, 1968).

(*a*) In La Tour du Valat (ca. 1600 acres) the following distinct habitats are present :

sansouire- composed of

1. *Salicornietum fruticosae.* Extensive plains covered particularly by *Salicornia fruticosa;*

2. Sea-lavender sward. Its vegetation is denser and richer in species. The most notable plant species are *Statice limonium* and *S. virgatum, Obione portulacoides* and *Sueda fruticosa.* The higher parts are covered by shrubs of *Phillyrea angustifolia;*

open marshes- overgrown partially with *Scirpus species* in summer and surrounded by a belt of *Juncus;*

marshes under reedbeds-mainly composed of *Phragmites communis* and *Typha angustifolia;*

edges- sides of dikes, ditches, etc., often with shrub vegetation;

dry agricultural land- grains, vineyards, grasslands, etc.;

wet agricultural land- rice fields.

Extensive agricultural land is situated to the east and southeast of La Tour du Valat.

(*b*) A few kilometres east of the Grand Rhône a gradual slope forms the zone of transition between the marshes of the Camargue and the stony plains of La Crau. From the marshes, dominated by *Scirpus* and *Phragmites* there is a gradual increase of *Cladium,* until the damp grasslands of *Molinia* mingled with *Isoëtus* and *Holoschoenus* are reached. These grade into the dry grasslands of *Brachypodium* which in turn give way to evergreen oak wood with *Quercus ilex.* Passing through the oak forest we reach the stony plains without woody vegetation, called the ‚Coussous', the genuine Crau. Here the vegetation is sparse, but florally rich in species. *Asphodelus fistulosus* and *Stipa capillata* are the most characteristic plants. Some agricultural land borders the marshes.

Throughout the Camargue and La Crau the prey fauna was rich in both species and numbers. In La Tour du Valat aquatic snakes were found in *Scirpus* marshes, reed marshes and rice fields; amongst the larger mammals rabbits were numerous.

At the time when pellets were collected in winter, ducks and other water birds, especially *Anas crecca,* were very numerous in the open wetlands, where they were intensively hunted by man. Many passerines inhabited the agricultural fields, especially the dry rice fields. Roadsides were frequented by small birds particularly after snowfall.

5. EVALUATION OF METHODS APPLIED.

In this explanation the utility of the methods (Chapter 3) will be discussed. Some authors (e.g. ROOTH, 1963 and THIOLLAY, 1968 and 1970) used a mixture of data of pellet analysis, analysis of prey remnants and other field observations to constitute a picture of the predation of a species in a particular area. This method can be used for a qualitative study only, and not for a quantitative study, as will be outlined below.

Nest observations.

By observing the nest from a hide, one gets a good picture of the prey items brought in by the adults for their young and most of the prey species can usually be recognized. However particular prey categories will never or seldom be recorded in this way, e.g. eggs, which are devoured on the spot, and carrion which can be to heavy too carry to the nest.

Prey remnants.

Collecting prey remnants on the nests leads to the same incomplete picture as the nest observations. Insects, frogs, lizards, young or small birds, and small mammals are often completely devoured and therefore leave no remains. Conversely, larger prey species like fish, snakes, larger birds, and larger mammals will be over-representated.

Pellets.

Pellets of the young on the nests never contained egg shells and seldom carrion, but traces of eggs and carrion have been found in pellets of the adult birds collected on the roosts. Other drawbacks of pellet analysis are :

(a) Quantification is difficult. Bones are largely digested by harriers. In the case of mice and voles it is possible to count the incisivae. However the presence of incisivae in pellets depends on the way the bird ate its prey. Has it devoured the whole prey or has it left the head or part of the head ? In the case of birds (feathers), rabbits and mammalian carrion (hairs) quantification is impossible. e.g. if one records Passeriforme feathers in a pellet it is seldom possible to determine if they originated from one, two or more birds, see note in Chapter 3.2.3.

Particular prey items are probably completely digested, e.g. eels and frogs, and seldom leave any remnants in pellets.

(b) Pellets, containing feathers, tend to be looser, and may easily be broken down by rain or contact with a wet surface, than the more compact, hairy pellets. This may bias the rate of birds to mammals in pellet analysis.

An advantage of pellet analysis in relations to prey remnant analysis, is the possibility to recover wholly eaten prey, like mice and voles, if the prey is not complety digestable.

In the Camargue, in 1969, one female *C.a.* disappeared and another neighboring female was found dead on its nest, both possible victims of poisoning. From that moment on the young of the first female were fed only by the male, who did not divide and feed the prey despite the fact that the young were unable to tear it into pieces and feed themselves. Consequently we visited the nest two or three times a day to feed the young from the food brought by the male and to collect pellets. In this way a comparison of prey actually consumed and pellet analysis was possible. In the period of 6-12 June, 1969, the two young consumed 42 prey items : 12 eels, 2 other fish, 7 frogs, 3 rats, 11 rabbits and 7 birds. In 13 pellets only rats (2 ×), rabbits (7 ×) and birds (8 ×) were recovered.

In a comparison of the relative prey frequencies, obtained in the Camargue in 1969, by nest observations, prey remnant analysis and pellet analysis (see Tables 6 and 7), one gets an impression about the over- and under-representation of particular prey categories. See Table 5.

Other field observations.

(a) Prey captures. In some cases it appeared to be possible to verify a capture by walking to the spot and identifying the remnants. In this way nest plundering, carrion eating and sometimes another prey capture could be checked. The prey carried away in the claws of the harrier could seldom be recognized. The size of the prey often could be estimated however.

Table 5: Comparison of relative prey frequencies in *C.a.*, **Camargue, 1969, in nest observations, prey remnant analysis and pellet analysis.** (See Tables 6 and 7).

	Prey remnants	Pellet contents
Over-represented in relation to nest observations	reptiles juv. and ad. Anatidae and Rallidae carrion	insects snakes juv. and ad. Anatidae and Rallidae carrion eggs
Under-represented in relation to nest observations	frogs pulli of nidifugous birds Passeriformes small mammals	fish frogs pulli of nidifugous birds Passeriformes
Not present in nest observations	carrion lizards	eggs

(b) Prey supply by the adults to the young or by the male to the female. It seldom appeared to be possible to recognize a prey in the talons of the birds; as in (a) the prey size often could be estimated.

Conclusions.

Undoubtly nest observations give the most reliable results in the study of prey selection in the breeding season. Prey remnants bias the predation picture as some prey categories do not leave any remains. The latter prey categories can be present again in pellets, but these do not give reliable quantitative results. Because of their different reliability values it is incorrect to combine data of nest observations, prey remnant analysis, pellet analysis, and other field observations in one list in order to get a total picture of prey selection. One has to consider these different data on their own relative merits. All of them are of importance because besides nest observations other types of field observation are required to get insight on predation on prey not carried to the nest. Food studies out of breeding season had to rely chiefly on pellet analysis.

6. FOOD IN BREEDING SEASON.

6.1. General comparison of food composition.

The observed prey species have been classified in 15 categories, relating to differences in size and habitat and to taxonomic differences. Data obtained through nest observations are shown in Table 6, data obtained by an analysis of prey remnants and pellets are shown in Tables 7, 8 and 9. Not all of the prey categories have been observed in each of the three harrier species :

Species	Prey categories not observed
C. aeruginosus	—
C. cyaneus	large insects, fish, frogs, snakes, bird eggs; lizards rare
C. pygargus	fish, snakes; frogs rare

Table 6: Prey data, relative frequencies, obtained by nest observations from a hide; highest frequencies in bold type. The two observation years in Flevoland have been kept separate because of the very different food.

Prey category	Ameland			Terschelling			Flevoland				Groote Peel	France			Total		
								C.c.				N.	S.				
	C.a.	*C.c.*	*C.p.*	*C.a.*	*C.c.*	*C.p.*	*C.a.*	1971	1972	*C.p.*	*C.p.*	*C.a.*	*C.a.*	*C.p.*	*C.a.*	*C.c.*	*C.p.*
1. Large insects	—	—	—	—	—	< 1	—	—	—	—	—	—	—	**64**	—	—	6
2. Fish	—	—	—	—	—	—	—	—	—	—	—	—	3	—	2	—	—
3. Frogs	—	—	—	—	—	< 1	—	—	—	—	—	—	8	—	4	—	< 1
4. Snakes	—	—	—	—	—	—	—	—	—	—	—	—	16	—	9	—	—
5. Lizards	—	—	—	—	< 1	**47**	—	—	—	—	—	—	—	3	—	< 1	26
6. Pulli of Anatidae and Rallidae	—	3	3	9	< 1	—	1	—	1	—	2	9	12	—	8	2	1
7. Juv. and ad. of Anatidae and Rallidae	10	—	1	—	—	—	4	1	—	—	—	5	5	—	4	2	< 1
8. Pulli and juv. of Limicolae; Phasianidae	10	31	10	26	8	2	**49**	13	**63**	15	2	—	1	5	17	20	5
9. Passeriformes	5	**34**	**43**	4	**66**	42	14	**49**	20	**67**	**70**	**73**	8	24	14	**48**	**43**
10. Small mammals	—	6	24	4	< 1	5	9	28	—	11	8	—	5	—	5	5	10
11. Larger mammals	**48**	15	3	**52**	24	< 1	14	6	8	6	2	9	**39**	—	**31**	18	1
12. Various prey	—	—	< 1	—	—	—	1	—	—	—	—	—	—	—	< 1	—	—
13. Unknown	29	9	17	4	1	4	9	3	7	2	17	5	4	3	5	5	8
Total number of prey	21	359	305	23	412	625	79	68	76	66	60	22	173	102	318	915	1.156
Number of nests observed	1	9	5	1	9	6	3	2	2	2	1	1	3*	2	6	22	16

(*) In two nests prey data were collected by nest observations. In a third nest the female dissappeared (see Chapter 5) and data of a complete series of prey items supplied by the male have been included in the Table.

Table 7: Relative prey frequencies in prey remnants (R) and pellets (P) in *Circus aeruginosus*; highest frequencies in bold type.

	Groote Peel		Flevoland 1971				Northern France				Southern France			
	R	P	R		P		R		P		R		P	
			nests	field	nests	field	nests	field	nests	field	nests	field	nests	field
1. Large insects	—	—	—	—	—	—	—	—	—	10	—	?	—	6
2. Fish	—	—	—	—	—	—	—	—	—	—	8	2	—	—
3. Frogs	—	—	—	—	—	—	—	14	—	—	—	4	1	2
4. Snakes	—	—	—	—	—	—	—	—	—	—	**40**	**38**	32	**33**
5. Lizards	—	—	—	—	—	—	—	—	—	—	—	4	—	—
6. Pulli of Anatidae and Rallidae	—	—	2	7	3	4	—	3	—	10	—	—	4	—
7. Juv. and ad. of Anatidae and Rallidae, ad. Limicolae	—	—	11	7	10	8	23	16	17	**20**	5	7	7	13
8. Pulli and juv. of Limicolae and Phasianidae	—	—	36	7	**38**	24	8	3	—	—	—	—	—	—
9. Passeriformes	13	25	11	14	7	4	**58**	**41**	**25**	**20**	6	5	2	4
10. Small mammals	—	**50**	—	—	3	—	—	—	—	—	2	—	4	12
11. Larger mammals	13	25	**40**	**64**	31	**36**	8	19	17	**20**	35	33	**34**	25
12. Various prey	**75**	—	—	—	—	—	4	—	17	10	2	4	2	—
13. Unknown	—	—	—	—	7	—	—	5	25	10	2	2	14	4
14. Carrion	—	—	—	—	—	—	—	—	—	—	—	2	—	—
15. Eggs	—	—	—	—	—	24	—	—	—	—	—	—	—	2
Total number	8	4	47	14	29	25	26	37	12	10	52	107	113	52
Number of pellets	—	4	—	—	18	13	—	—	5	7	—	—	55	25
Number of nests	—	—	12	—	12	—	3	—	3	—	4	—	4	—

Table 8: Relative prey frequencies of prey remnants (R) and pellets (P) in *Circus cyaneus*; highest frequencies in bold type.

	Terschelling	Flevoland		Northern France		
	R	R	P	R		P
	nests	nests	nests	nests	field	nests
7. Juv. and ad. of Anatidae and Rallidae	—	11	10	—	—	—
8. Pulli and juv. of Limicolae and Phasianidae . . .	14	11	—	—	**67**	—
9. Passeriformes . . .	**86**	**78**	**40**	**50**	33	**67**
10. Small mammals . . .	—	—	20	**50**	—	—
11. Larger mammals . . .	—	—	28	—	—	33
12. Various prey	—	—	—	—	—	—
13. Unknown	—	—	3	—	—	—
14. Carrion	—	—	—	—	—	—
15. Eggs	—	—	—	—	—	—
Total number	17	9	40	2	3	3
Number of pellets . .	—	—	17	—	—	2
Number of nests . .	7	2	2	1	—	1

Table 9: Relative prey frequencies of prey remnants (R) and pellets (P) in *Circus pygargus*; highest frequencies in bold type.

	Terschelling	Flevoland				Groote Peel		N. France		Southern France			
		R		P		R	P	R		R		P	
	R	nests	field	nests	field			nests	field	nests	field	nests	field
1. Large insects	—	—	—	—	—	—	—	**67**	—	**80**	—	24	**50**
2. Fish	—	—	—	—	—	—	—	—	—	—	—	—	—
3. Frogs	—	—	—	—	—	—	—	—	—	—	—	—	—
4. Snakes	—	—	—	—	—	—	—	—	—	—	—	—	—
5. Lizards	—	—	—	—	—	—	—	—	—	—	—	5	—
6. Pulli of Anatidae and Rallidae	—	—	—	—	—	—	—	—	—	—	—	—	—
7. Juv. and ad. of Anatidae and Rallidae	3	7	—	—	3	—	—	—	—	—	—	—	—
8. Pulli and juv. of Limicolae and Phasianidae	—	7	—	—	—	—	—	—	—	—	—	—	—
9. Passeriformes	**89**	**73**	**100**	**54**	**59**	**100**	**47**	33	**100**	20	**100**	**65**	—
10. Small mammals	—	7	—	26	13	—	44	—	—	—	—	5	**50**
11. Larger mammals	3	7	—	14	11	—	—	—	—	—	—	—	—
12. Various prey	5	—	—	—	—	—	—	—	—	—	—	—	—
13. Unknown	—	—	—	6	5	—	—	—	—	—	—	—	—
14. Carrion	—	—	—	—	—	—	—	—	—	—	—	—	—
15. Eggs	—	—	—	—	8	—	8	—	—	—	—	—	—
Total number	28	15	14	35	37	2	36	3	2	5	3	37	2
Number of pellets	—	—	—	21	24	—	23	—	—	—	—	24	1
Number of nests	4	4	—	4	—	—	—	1	—	2	—	2	—

As the totals are composed of data from different study areas it is not permissable to draw any important conclusions on the prey selection. However, one has to consider harrier predation and food in each study area.

6.2. Comparison of food composition in different areas.

Circus aeruginosus (Tables 6 and 7).

Important prey categories in the food of *C.a.* were young Limicoles and Phasianidae and larger mammals, the first mentioned prey in Terschelling and Flevoland, the latter in all of the study areas except Northern France. Snakes and young water birds were frequently taken in Southern France. The snakes taken were mainly *Natrix natrix* and *Natrix maura*, both aquatic species. In Ameland the percentage ‚unknown' was relatively high, but probably mainly comprised young nidifugous land birds of prey category 8. In Southern France the amount of nidifugous land birds in the food was strikingly low. Generally, aquatic prey species were more preyed upon in Southern France than elsewhere.

The situation in Northern France was exceptional by the preponderance of Passeriforme birds, though pellets and prey remnants contained relatively more water birds and larger mammals (Table 7). The latter are from all nests combined and demonstrate a too small percentage of small prey (Chapter 5).

Very little data are available from the Groote Peel. In the area prey remnants of juvenile *Larus ridibundus* were very regularly found.

Several field observations are available of Marsh Harriers eating eggs at the nests of ducks (Flevoland, Southern France) and gulls (*Larus ridibundus*, Groote Peel). Large insects were present in pellets only. Carrion, eggs and large insects have not been observed being brought to the young on the nest, though a few times I observed a male supplying carrion to his mate. Still the feeding of eggs to the young on the nest appears to occur, as it has been recorded by TEN KATE (1930).

The heaviest prey items observed included half-grown or nearly full grown pheasants in Flevoland, adult ducks of the species *Anas platyrhynchos* in Flevoland (may have been sick, moulting or wounded birds), large rabbits in Terschelling, the Camargue and Flevoland. Carrying those items to the nest was sometimes difficult and often the birds had to rest on the ground at intervals. With one notable exception, prey animals brought to the nest were dead and often had been partly devoured. On one occasion however an *Emberiza schoeniclus* pullus was brought to the nest quite intact by a male Marsh Harrier, and piped continually until the female came to divide it up for feeding.

In the Camargue I once observed a female seizing a snake (*N. natrix*) which appeared on the nest while the bird was feeding the young. Snakes were often wriggling fiercely when taken to the nests, and occasionally in their convulsions they managed to swing their bodies around a wing or another part of the body of a young bird. Considerable effort was required to extricate themselves and it seems not impossible that young birds may perish in this manner, as they may throw themselves from the nest in their struggles.

Predation on large insects during the breeding season could not be established with certainty in all cases. In several Marsh Harrier territories in Southern France carapaces of 38 *Hydrous piceus* (Coleoptera) were discovered. Magpies (*Pica pica*), numerous in the same area cannot be held responsable for this, as *Hydrous piceus* only incidentally occurs in the Magpies' diet in Camargue (BIGOT, 1966). Occasionally I saw in Camargue Marsh Harriers seizing and devouring small objects near the waterside, but eating of *Hydrous piceus* could not be proved. GLUTZ VON BLOTZHEIM *et al.* (1971) records *Hydrous piceus* as a possible prey species.

Circus cyaneus (Tables 6 and 8).

Passeriformes constituted an important prey category in all of the study areas. In addition in Ameland and Flevoland pheasants were important, large mammals in Ameland and Terschelling. Small mammals were taken in relatively great numbers only in Flevoland in 1971.

In Terschelling the very heavy predation on Passeriformes seems to have been counterbalanced by the small number of nidifugous young birds and small mammals in the diet. In Flevoland, 1971, the amount of larger mammals was relatively low, the number of small mammals relatively high (see above) and of nidifugous young birds in between the percentages of Ameland and Terschelling. In 1972 numerous pheasants were supplied to the young instead, but no small mammals as in 1971 and relatively few Passeriformes. No eggs and carrion were observed in the food throughout.

The heaviest prey observed included half-grown or nearly full-grown pheasants in Flevoland.

Circus pygargus (Tables 6 and 9).

In almost all of the study areas Passeriformes constituted the most frequently observed prey category, but in Southern France large insects were taken more often. Lizards were observed in Terschelling more than elsewhere, even than in Southern France. In Ameland where lizards do not occur, small mammals and young nidifugous birds occurred in the diet in numbers comparable to those of lizards in Terschelling.

Remains of small eggs were occasionally present in pellets. Once a complete and unbroken egg of *Alauda arvensis* was found in a pellet. This seems not unusual, as MARTENS (1964) found 6 unbroken eggs of this species in a gizzard of *C.p.*

In the years that *C.p.* has been studied we did not observe them eating carrion, although once, in 1972, in Flevoland, a male was observed on a dead hare.

Analysis of prey remnants and pellets confirmed on the whole, the results of the nest observations. In Terschelling pellets of *C.p.* containing lizard scales were found.

The heaviest prey observed included a half grown pheasant and small rabbits in Flevoland, the latter of which were often supplied to the nestlings, divided by the adults. Twice I observed living prey taken to the nest by the female : downy chicks of *Charadrius species* and *Recurvirostra avocetta*, respectively in Flevoland.

Comparison of *C.a.*, *C.c.* and *C.p.*

C.a. : Water birds, chiefly consisting of Anatidae and Rallidae were most often taken by *C.a.*, least by *C.p.* In Flevoland young pheasants and Limicolae were important. The number of Passeriformes and small mammals were very low elsewhere. As mentioned above, the situation in Northern France were peculiar. Predation on fish and snakes was only observed in Southern France.

C.c. : To some extent, as in *C.a.*, young pheasants and Limicolae were important, and Passeriformes as in *C.p.* The data obtained in 1972 in Flevoland were interesting in that young pheasants were taken to such an extent that the percentage of Passeriformes in the food was considerably diminished (see Chapter 9.2.1.).

C.p. : Passeriformes formed the predominant food. In relation to *C.c.* and *C.a.* the percentage of young nidifugous birds was very low. Lizards and large insects were frequently taken in some areas, and never found to such an extent in the other harrier species. Larger mammals were relatively rarely taken.

Interspecific overlap in predation on the same prey or prey category occurred in different areas. It can be seen in Table 6 that the most important overlap in Ameland, Terschelling and Flevoland was found in the prey categories 8, 9, 10 and 11. These categories will be considered in more detail.

Young Limicolae and Phasianidae

These prey types, consisting mainly of young waders and pheasants, were supplied by all three harrier species, particularly in Ameland and Flevoland. The percentages in nest observations are shown in Table 12.

Generally the pheasants supplied by *C.p.* to the nests appeared to be smaller than those supplied by *C.c.* and *C.a.*, but no size differences were noticed between pheasants taken by *C.c.* and *C.a.*

Passeriformes.

In several areas an important overlap was present in the number of Passeriformes taken by the three harrier species, especially by *C.c.* and *C.p.* (Table 6). However, one has the problem of age differences in the birds taken. The ages were not recorded every year in the course of this study, so only some data are available. In Table 10 « pulli » and

Table 10: Frequencies of Passeriformes in the prey records; n-values concern 100%.

Locality and year	*C.p.*			*C.c.*			*C.a.*		
	pulli	juv./ad.	n =	pulli	juv./ad.	n =	pulli	juv./ad.	n =
Terschelling 1959	10	33	171	0	70	46	0	4	23
Groote Peel 1965	17	53	60	—	—	—	—	—	—
Flevoland 1971, 1972	42	24	66	4	29	144	5	9	79
Northern France 1970	—	—	—	—	—	—	27	45	22
Southern France 1969	3	21	102	—	—	—	8	0	173

«juvenile or adult» (juv/ad) have been distinguished. Even when observing from a hide apparently unnoticed by the birds however, it was difficult to distinguish whether the partly plucked and occasionally decapitated prey brought to the nest was an advanced juvenile or an adult bird.

The data includes juvenile and adult Starlings (*Sturnus vulgaris*), which were not taken in corresponding amounts by the three species; this is shown by the following data on the relative frequency of the species as a prey, expressed as a percentage of the total number of Passeriformes in each species :

C.p. — 1.3% (n = 8);
C.c. — 13.8% (n = 32);
C.a. — 4.5% (n = 2).

Although the overlaps appear to be reduced in this way, an important overlap is still present in the predation on Passeriformes, especially in *C.c.* and *C.p.* (Table 12).

Small mammals.

Among small mammals voles were most important, especially *Microtus arvalis* (not present in Terschelling). Prey percentages of voles are presented in Table 12.

Larger mammals.

This prey category was important in *C.a.* and *C.c.* especially in Ameland and Terschelling, and was composed almost entirely of young rabbits (Table 6). An attempt was made to compare the size of the rabbits by measuring the length of hind foot, using both remains and intact prey (before it was fully quartered) that was found on or near the nests. The results obtained may not fully reflect the size of the rabbits taken due to the following problems :

1. the smaller hind legs will be swallowed more readily than larger ones, effecting the proportions found among prey remnants;
2. *C.a.* presumably is able to swallow larger hind legs than C.c.;
3. in situations of abundant food less rabbit legs tend to be swallowed than in cases of food shortage.

Table 11: Lengths of hind feet of rabbits, taken by *C.a.* and *C.c.* in the Netherlands.

Length of hind foot (mm)	C.*a*.	C.*c*.
30-40	1	—
40-50	—	—
50-60	12	10
60-70	3	3
70-80	—	—
80-90	1	—
n =	17	13
median length	57	54

The measurements of the hind feet are shown in Table 11, but no significant differences between the species were found.

The prey percentages of the most important prey categories in Ameland, Terschelling and Flevoland 1971 are presented in Table 12. In the same Table the relative importance of these prey categories is shown as the percentage of the total weight of all observed prey. For estimated prey weights see Appendix 8; data on prey weights were obtained from Niethammer (1937-1942), Van den Brink (1968), by my own measurements and additional calculations. If prey weights are considered it will be clear that overlap in the absolute amount of the prey will be enlarged in heavy prey (e.g. rabbits) and reduced in the light prey (e.g. voles and Passeriformes).

6.2.2. *Intraspecific comparison.*

As seen by various authors and with respect to several species of avian predators, sexual dimorphism in birds of prey can be correlated to predation differences between males and females (storer, 1966 Reynolds, 1972). Intraspecific differences in predation may give a deeper insight in the significance of interspecific differences in the three harrier species. Intraspecific differences were studied in Ameland

Table 12: Interspecific comparison of predation on the most important prey categories, shown in percentages of prey numbers (upper rows) and estimated biomass (lower rows). If the distinction between pulli and juveniles or adults was not noticed during the nest observations, the relative numbers have been estimated according to Table 10.

Prey category	Ameland			Terschelling			Flevoland 1971		
	C.p.	*C.c.*	*C.a.*	*C.p.*	*C.c.*	*C.a.*	*C.p.*	*C.c.*	*C.a.*
Limicolae pulli	5	17	0	2	5	26	8	4	0
	9	14	0	7	4	8	6	2	0
Pheasants	6	13	10	0	3	0	8	9	49
	7	14	5	0	3	0	9	18	40
Passeriformes, pulli and Starlings not included	34	30	0	33	57	2	24	22	9
	20	7	0	47	17	< 1	17	10	2
Passeriformes pulli	8	0	0	8	0	2	42	4	5
	4	0	0	8	0	< 1	20	1	1
Voles	23	6	0	0	0	0	11	26	4
	14	2	0	0	0	0	7	12	1
Rabbits	2	15	48	< 1	24	52	6	6	13
	14	41	65	2	69	81	37	26	24
Other and unknown prey	21	19	43	56	12	17	1	28	20
	32	22	30	35	7	10	4	33	33

(1967 and 1970), Terschelling (1962 and 1968), Flevoland (1971 and 1972), Groote Peel (1965) and Southern France (1969). From Terschelling (1962) incomplete data are available and have to be considered separately. The results of these studies have been included in the data of Chapter 6.2.1., but are now considered in detail (Table 13). The data have been revised in the same way as in Chapter 6.2.1. More detailed prey percentages are shown in Table 14.

The percentages of Passeriformes «pulli» and «juvenile or adult without Starlings» have been based on the values discussed in Chapter 6.2.1.

Circus aeruginosus.

In Flevoland males took fewer young pheasants and more Passeriformes than did females. In the Camargue snakes were taken only by males. In addition, apart from nest observations, snake-carrying males were observed 23 times, but it was never ascertained that a female carried a snake. Songbirds and small mammals were supplied only by males, whereas young water birds (category 6) were taken mainly by females. Rabbits were taken in about equal amounts by males and females. In Ameland (1964) and Northern France (1970) there was evidence that prey observed at the nests were probably supplied by the female (Table 6).

Circus cyaneus.

The most striking intraspecific differences existed in predation on Passeriformes and rabbits (larger mammals). In Ameland, Terschelling and Flevoland females took more rabbits (more mammals), whereas males took a higher rate of Passeriformes. Females also supplied somewhat more pheasants, especially in Ameland.

Circus pygargus.

Interpretation of the prey data is considerably impeded by the high percentage of ‚unknown' in Ameland and the very low prey numbers in some other cases.

In all study areas but one, Flevoland, females were found to take more mammals than did males, especially small mammals. However this seems to be true only when the total of mammals is taken into account. In Flevoland females took relatively more rabbits than did males, but males on the other hand supplied the highest percentage of voles.

Again in all areas but Flevoland, the males took more nidifugous land birds (category 8) and were found everywhere to supply more Passeriformes.

Unfortunately in 1968 in Terschelling only one lizard was recorded as being supplied among a very low number of prey items. From 1962 it appeared that females supplied more lizards than did males.

In Southern France the female supplied a great number of large insects.

Comparison of C.*p.*, C.*c.* and C.*a.* (See Table 14 and Figure 2).

In conclusion, C.*a.* males supplied more small prey and less nidifugous land and water birds than females; males and females both supplied rabbits. In C.*c.*, males supplied more Passeriformes, females more rabbits. In C.*p.*, males supplied more birds (Passeriforme and nidifugous land birds), females more mammals, large insects and more lizards.

With regard to intraspecific differences females supplied more mammals in C.*c.* and C.*p.*, males more in C.*a.*

Comparing C.*a.* to C.*c.* with special reference to the prey categories in Table 14, the largest overlap appeared to occur in C.*c.* females and C.*a.* males (rabbits, voles, Passeriformes and in Flevoland pheasants).

Table 13: Percentage of prey numbers, supplied to the nest young.

	Circus aeruginosus						*Circus*		
	Flevoland 1971			Southern France [1])			Ameland 1967, 1970		
Sex and numbers	2 ♂♂	3 ♀♀	Σ	3 ♂♂	2 ♀♀	Σ	6 ♂♂	6 ♀♀	Σ
1. Large insects	—	—	—	—	—	—	—	—	—
2. Fish	—	—	—	4	13	4	—	—	—
3. Frogs	—	—	—	12	6	8	—	—	—
4. Snakes	—	—	—	22	—	16	—	—	—
5. Lizards	—	—	—	—	—	—	—	—	—
6. Anatidae, Rallidae, pulli	3	—	1	3	31	12	2	5	4
7. Anatidae, Rallidae, juv./ ad., Limicolae ad. .	3	9	4	4	6	5	—	1	< 1
8. Limicolae pulli/juv., Phasianidae . . .	30	64	49	2	—	1	27	38	35
9. Passeriformes . . .	27	—	14	13	—	8	44	21	29
10. Small mammals . .	15	—	9	6	—	5	11	4	6
11. Larger mammals . .	12	9	14	34	31	39	7	24	17
12. Sundries	—	9	1	—	—	—	—	—	—
13. Unknown	9	9	8	1	13	4	9	7	8
Total number . . .	33	11	79	101	16	173	131	185	316

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[1]) See note under Table 6.

cyaneus

Terschelling						Flevoland					
1962			1968			1971			1972		
2 ♂♂	2 ♀♀	Σ	4 ♂♂	4 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	2	2	—	—	—	—	—	—
—	—	—	7	5	5	—	—	—	—	4	1
—	—	—	—	—	—	—	5	2	—	—	—
15	—	7	20	18	19	11	15	13	73	48	64
69	12	57	53	36	41	55	40	49	23	26	20
—	—	—	—	5	3	32	25	28	—	—	—
15	88	33	20	34	31	—	10	6	—	22	8
—	—	—	—	—	—	—	—	—	—	—	—
—	—	4	—	—	—	2	5	3	5	—	7
39		145	15	44	59	44	20	68	40	23	76

(Table 13 : continuation)

Circus

	Ameland, 1967, 1970			Terschelling					
				1962			1968		
Sex and numbers	4 ♂♂	4 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ	1 ♂	1 ♀	Σ
1. Large insects	—	—	—	—	—	—	—	—	—
2. Fish	—	—	—	—	—	—	—	—	—
3. Frogs	—	—	—	—	—	—	—	—	—
4. Snakes	—	—	—	—	—	—	—	—	—
5. Lizards	—	—	—	66	76	58	—	6	4
6. Anatidae, Rallidae, pulli	1	7	4	—	—	—	—	—	—
7. Anatidae, Rallidae, juv./ ad., Limicolae ad. .	—	—	—	—	—	—	—	—	—
8. Limicolae pulli/juv., Phasianidae . . .	19	6	16	1	1	1	33	12	19
9. Passeriformes . . .	49	20	39	32	21	34	67	65	66
10. Small mammals . .	14	40	21	1	1	4	—	18	12
11. Larger mammals . .	3	2	3	—	—	< 1	—	—	—
12. Sundries	—	—	—	—	—	—	—	—	—
13. Unknown	14	26	17	—	—	3	—	—	—
Total number . . .	129	103	232	98	80	248	9	17	26

ygargus

Flevoland 1971			Groote Peel			Southern France		
2 ♂♂	2 ♀♀	Σ	1 ♂	1 ♀	Σ	2 ♂♂	2 ♀♀	Σ
—	—	—	—	—	—	25	87	64
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	6	2	3
—	—	—	2	—	2	—	—	—
—	—	—	—	—	—	—	—	—
6	43	15	2	—	2	14	—	5
73	43	67	70	67	70	50	7	24
14	—	11	6	22	8	—	3	2
4	14	6	2	—	2	—	—	—
—	—	—	—	—	—	—	—	—
2	—	2	18	11	17	6	2	3
49	14	66	50	9	60	36	61	102

Table 14: Inter- and intraspecific comparison of predation on the most important prey categories, expressed in percentages of numbers.

	Ameland 1967/70				Terschelling 1962				Terschelling 1968				Flevoland 1971					
Prey category	*C.p.*		*C.c.*		*C.p.*		*C.c.*		*C.p.*		*C.c.*		*C.p.*		*C.c.*		*C.a.*	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Limicolae, pulli	8	2	21	18	1	1	15	0	33	12	20	18	0	36	5	5	0	0
Pheasants	12	3	6	20				0	0	0	0	0	6	7	7	10	30	64
Passeriformes, pulli and Starlings not included	36	16	43	18	25	17	69	12	44	59	53	36	25	29	32	5	15	0
Passeriformes, pulli	9	4	0	0	6	4	0	0	11	12	0	0	49	14	7	0	12	0
Voles	14	37	10	4	0	0	0	0	0	0	0	0	14	0	30	25	3	0
Rabbits	3	2	7	23	0	0	15	88	0	0	20	33	4	14	0	10	12	9
Other and unknown prey	19	37	14	16	0	0	0	0	11	18	7	12	2	0	20	45	27	27
Total number	129	103	131	185	98	80	39		9	17	15	44	49	14	44	20	33	11

Comparing C.*c.* to C.*p.* in Ameland and Flevoland, the largest overlap was present in the food of C.*p.* males and C.*c.* males, but this was not strikingly larger than the overlap in food of C.*p.* males and C.*c.* females. Comparing C.*p.* to C.*a.* food composition of C.*p.* males and females both showed little overlap with C.*a.*

7. FOOD OUTSIDE BREEDING SEASON.

Outside the breeding season prey data could be collected only by analysis of pellets of C.*a.* and C.*c.*, collected at communal roost sites, and also by field observations. A comparison has been made with published data on pellets, prey remnants and stomach contents. In C.*p.* food data outside of the breeding season was particularly scarce.

7.1. THE MARSH HARRIER, *Circus aeruginosus.*

Pellets were collected at communal roosts near the Etang de Vaccarés in the Camargue, in December 1970, where around 20 Marsh Harriers roosted together. The result of the analysis is shown in Table 15. The pellets contained mainly aquatic and marsh animals, with birds predominating, particularly Anatidae. It appears from our field observations that attacks on Anatidae, mainly *Anas crecca* and *Anas platyrhynchos*, were invariably directed at disabled or sick birds, most of them probably bearing shotgun wounds. The hunting behaviour

Table 15: Contents of 214 pellets of C.*a.*, collected at a communal roost in Southern France, December 1970.

Prey category	Percentage of number of prey records	
Large insects	8	
Fish	< 1	
Reptiles	1	
Birds total	75	
Egretta garzetta		< 1
Anatidae		56
Galliformes		< 1
Rallidae		7
Limicolae		1
Passeriformes		11
Unknown birds		1
Mammals total	16	
Rabbit/Hare		2
Arvicola sp.		1
Rattus sp.		1
Myocastor coypus		1
Soricidae		< 1
Mouse or vole		10
Total number of prey records	272	

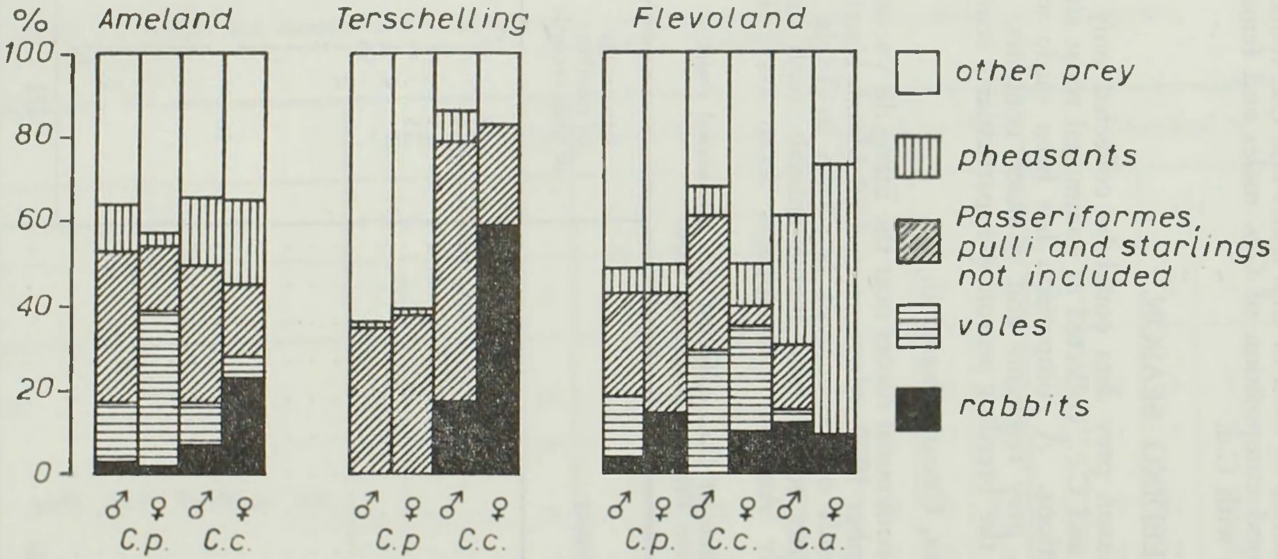


Fig. 2. — Prey percentages of the most important prey categories from Table 14.

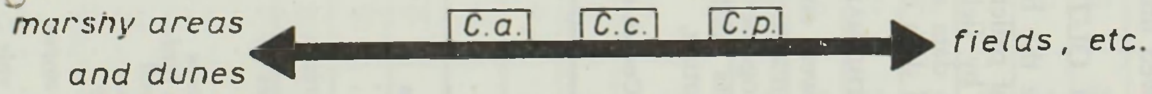


Fig. 3. — Comparison of habitat preference, indicated by food composition only.

with respect to *Anas crecca* has been described by Tamisier (1970), who also concluded that predation was directed particularly towards wounded individuals. Eating of carrion has regularly been observed. The remnants of *Egretta garzetta* in one of the pellets likewise probably refer to a sick bird or even a corpse.

The relatively high percentage of Passeriformes in the pellets corresponds to the great abundance of buntings and finches in the Camargue in December 1970 and January 1971. Bones were scarce in the pellets and only 5 bills (corresponding to 2.3%) of buntings, finches and/or sparrows were found. In one pellet (0.5%) remnants of a Starling, *Sturnus vulgaris*, could be recognized.

The few remnants of *Myocastor coypus* possibly refer to carrion also. Only young specimens can be taken alive. *Myocastor coypus* was numerous in the marshes, but during a period of frost in January 1971 many of them perished, and before decomposing were often found partially eaten by harriers.

Some winter food data of Thiollay (1970) from the Camargue mentions ducks and other water birds, 1 *Buteo buteo*, 2 *Pica pica*, 3 *Corvus monedula*, and 1 *Vulpes vulpes*, the majority of which probably had been taken when these animals were wounded or dead. Winter food data from Spain (Ebro delta, December) and Italy (December-April) also indicate the importance of water animals; in Hungary (September-February) mammals predominated. In NW Congo circumstances are considerably different from Southern Europe, and little data were available. See Table 17.

The number of Passeriformes recorded was low in all of the above mentioned areas.

Bakker (1955) observed *C.a.* to be uncommon in Noordoostpolder, Netherlands, in winter and concluded that the harriers each took 5-6 voles (*Microtus arvalis*) a day on the average. Dement'ev (1966) mentions winter prey in Talysh which includes carrion, wounded birds, various water birds, e.g. rails and snipe, fish, small rodents; in SW Turkmenia principally waterfowl, small rodents, lizards and fish.

7.2. THE HEN HARRIER, *Circus cyaneus*.

Pellets were collected at communal roosts in Terschelling (ca. 15 birds), Lauwerspolder (ca. 30 birds), and Flevoland (1970 : ca. 50 birds; 1971 : ca. 30 birds). The data, presented in Table 16, show two different types of food. In Lauwerspolder and Flevoland 1970, where *Microtus arvalis* was very numerous, the amount of these voles in the food was very high, while that of birds was comparatively low. Accordingly, in Flevoland (1970), all 24 prey captures observed involved voles. In Terschelling where voles are lacking and in Flevoland (1971), when the *Microtus arvalis* population was at a relatively low level, bird remains predominated. In Terschelling Starlings were recognized in 45.7% of the total of Passeriformes found in the pellets.

Table 16: Contents of pellets of *C.c.* from various localities.

Prey category	Percentage of number of prey records			
	Terschelling	Flevoland		Lauwerspolder
	January 1970 70 pellets	January March 1970 417 pellets	January February 1971 110 pellets	February 1971 50 pellets
Birds total	63	7	49	8
Anatidae	—	3	—	—
Phasianidae	2	1	—	—
Rallidae	1	2	—	—
Limicolae	2	1	—	—
Passeriformes	58	< 1	—	—
Unknown birds	—	< 1	—	—
Mammals total	37	93	51	92
Rabbit/Hare	11	< 1	—	—
Rattus sp.	—	< 1	—	—
Sorex araneus	2	< 1	—	—
Microtus arvalis (*)	—	87	37	92
Micromys minutus	—	5	14	—
Apodemus sylvaticus	11	—	—	—
Other-unknown mice	12	—	—	—
Total number of prey records	90	453	123	52

(*) May include a few *Microtus agrestis*.

All these data suggest that *C.c.* shows a preference for voles wherever these are numerous, but when necessary they can switch over to Passeriforme birds.

Also Hamerstrom (1969) noted that for the American Marsh Hawk (*Circus cyaneus*) a scarcity of voles during the breeding season is important as it leads to increased feeding on birds; there existed a close agreement between harrier productivity and vole abundance.

Various scources in the literature also give evidence of a preference of *C.c.* for *Microtus arvalis* in winter, some of which will be cited below and in Table 17.

In Baye de l'Aiguillon, France, in winter 1965-1966, when the population of *Microtus arvalis* was at a maximum, fewer Passeriformes were recorded as food of *C.c.*, compared with the winter before. Similarly during a plague of *Microtus arvalis* in Kent, Gilham (1955) observed many Hen Harriers. In Italy, where *Microtus arvalis* only occurs locally in the north, and other diurnal rodents are not accessible, Passeriformes are the most important food for wintering *C.c.* In the stomachs of *C.c.* collected in Hungary and Yugoslavia many *Microtus arvalis* were found amongst other small mammals and Passeriformes.

Wassenich (1968) supposed prey of *C.c.* in Luxembourg to be small mammals. Successful catches of small birds were not observed.

7.3. The Montagu's Harrier, *Circus pygargus*.

As *C.p.* spends the winter mainly in tropical Africa, we did not collect data on their winter food. Besides, winter prey data on *C.p.* have been very rarely recorded, but includes mainly insects and lizards (see : Glutz von Blotzheim *et al.* 1971). On arrival at their still snow-covered ranges in the Kirgiz steppe, eating of carrion has been observed (Suschkin, 1908, in Glutz von Blotzheim *et al.* 1971). Evidence of *C.p.* frequently taking Passeriformes is not apparent throughout the literature. In Kenya C. Smeenk (pers. comm.) observed some captures of small ground birds, but in agricultural land great densities of wintering harriers may indicate a preference for small mammals (Smeenk dit not visit locust-rich areas).

For data on food of migrating harriers in Southern Europe : see Table 17.

A thorough study of the winter food of *C.p.* would be worthwhile and could be made, for example, by analysing pellets collected at communal roosts.

7.4. Comparison.

Although winter food data are comparatively scarce, some striking interspecific differences are apparent. *C.a.* appears to prey a great deal on marsh animals, often of considerable size, and probably frequently includes sick or otherwise disabled animals and carrion. Heavy predation on voles has only been suggested by Bakker (1955), although this has never been confirmed by subsequent systematic food studies.

C.c. appeared to prefer *Microtus arvalis*, wherever abundant, but is capable of taking large numbers of Passeriform birds when voles are not available.

In its African winter quarters *C.p.* seems to take mainly small prey, like large insects and lizards, but possibly also other small ground animals.

More information on the winter food of *C.a.* and *C.p.* in Africa is required. Possibilities for studying intraspecific sexual differences in prey selection in winter were not found.

8. SELECTION OF HUNTING HABITATS.

This chapter deals with the problem of whether and to what extent prey composition can tell us something about the selection of hunting habitat. As a discussion on hunting will be restricted to another paper, we will only deal here with a comparison of the prey composition of the harrier species and the prey densities recorded in distinct habitats

Table 17 : Survey of published winter food data.

Legend : 1 = Thiollay, 1968; 2 = Moltoni, 1937; in Glutz von Blotzheim, *et al.*, 1971; 3 = Bittera, 1914; 4 = Chapin, 1932; in Glutz von Blotzheim, *et. al.*, 1971; 5 = Dickson, 1970; 6 = Glutz von Blotzheim, *et. al.*, 1971; 7 = Castroviejo, 1968 in Glutz von Blotzheim, *et al.*, 1971; 8 = Bittera, 1914 and Czornoi, 1959 in Glutz von Blotzheim, *et al.*, 1971.

All stomach data and prey remnants represent actual prey; presentation of prey numbers from pellets is unknown.

Prey category	*Circus aeruginosus*				*Circus cyaneus*					*Circus pygargus*	
	1	2	3	4	5	1 & 6		2	8	7	3
	Spain	Italy	Hungary	Congo	Scotland	Vendée	France	Italy	Hungary & Yugo-slavia	Spain	Hungary
	pellets and prey remnants	37 stomachs	15 stomachs	6 stomachs	32 pellets	1964/65 pellets	1965/66	19 stomachs	67 stomachs	4 stomachs	12 stomachs
Insects	—	≥ 3	—	1	—	—	—	—	—	49	≥ 6
Fish	8	2	—	—	—	—	—	—	—	—	—
Frogs and toads	3	5	—	—	—	—	—	—	—	—	—
Lizards	—	1	—	4	—	—	—	—	—	—	1
Anatidae	7	2	—	—	—	—	—	—	—	—	—
Phasianidae	—	—	1	—	—	—	—	—	9	—	1
Rallidae	—	9	—	1	—	—	—	1	—	—	—
Limicoles	2	—	—	—	2	1	—	—	—	—	—
Passeriformes	5	3	1	—	32	37	13	12	39	—	—
Other and unknown birds	2	12	5	—	3	—	—	5	7	—	3
Small mammals	5	7	2	1	4	23	515	10	57	—	1
Larger mammals	4	—	16	—	—	—	—	1	—	—	1
Carrion (dolphin)	1	—	—	—	—	—	—	—	—	—	—
Bird eggs	—	—	—	5-6	—	—	—	—	—	—	—

(Table 4). As prey densities have only been roughly estimated, only some general observations can be made.

The assumption has been made that harriers prey where they find a particular prey species in its highest densities.

Ameland.

As *C.a.* supplied a higher percentage of water birds than did the other harriers, *C.a.* must have frequented wet habitats more than did the other species. However the total number of prey items observed in *C.a.* was low. The other two species of harrier may have taken Passeriformes in reed marshes as well as in their drier habitats. As some reed inhabiting Passeriformes were present in the food of *C.c.* and *C.p.* as well (e.g. *Emberiza schoeniclus*; also *Sturnus vulgaris*, which may have been captured in reedbeds at their roosts), these harriers seem to have at times also hunted over reed marshes. Still *C.p.* supplied relatively more Passeriformes inhabiting open fields (e.g. larks) than did *C.c.*, suggesting that *C.p.* also frequented the cultivated area.

Largest numbers of young Limicolae and Phasianidae were taken by *C.c.*, indicating that this species had been hunting over sand dunes and meadows. *C.p.* supplied the highest percentage of voles, which it must have taken in dry dune valleys or meadows. In 1967 voles were often supplied by the females and at very short intervals, which suggests that they were captured in the vicinity of the nest in the dunes.

Most of the rabbits were supplied by *C.a.* These must have been mainly caught in the land dunes, where they were also regularly captured by females of *C.c.*

Terschelling.

The few Limicolae captured by *C.a.* probably originated from the cultivated area or Boschplaat. Rabbits may have been preyed upon by *C.a.* and *C.c.* (particularly females) in the dunes.

High percentages of Passeriformes in the food of *C.c.* and *C.p.* suggest that these species have been frequently hunting in the dunes. As in Ameland *C.p.* supplied relatively more field inhabiting Passeriformes (larks)., which probably have been captured in the meadows in the cultivated area or in the Boschplaat.

Lizards captured by *C.p.* probably originated exclusively from the dunes. The short intervals between the capture of prey items also indicates that they had been taken not far from the nest.

The numerous Passeriformes, especially Starlings, taken in winter, could have been taken all over the island, but their roosts may have been particularly attractive to harriers.

Flevoland.

As in Ameland, the presence of water birds in the food of *C.a.* points to hunting in reed marshes, where other important prey items common in the food of *C.a.* can be caught. In addition, open field inhabiting species, like larks and voles, have been recorded in the food of *C.a.* males.

Small songbirds, supplied by *C.c.* and *C.p.* (especially larks) suggest that these species had been hunting over crops and verges, but reed inhabiting birds (*Emberiza schoeniclus*, *Panurus biarmicus*, *Acrocephalus species*) have also been supplied by *C.c.* As in Ameland and Terschelling, most Passeriformes supplied by *C.p.* were larks. More voles were supplied by males than by females of both *C.c.* and *C.p.*, which made us think that males had more frequently been hunting in the open fields than females.

The winter food composition of *C.c.* suggested different main habitat selection in 1970 and 1971. Pellet examination in 1970 showed mostly voles, which probably had been captured in the open fields; in 1971 we found many more birds and *Micromys minutus* instead, suggesting that during this winter the harriers had been frequently hunting in the reed marshes, rather than in the open fields, where, incidentally, voles were scarce now.

Groote Peel.

Whereas *C.a.* frequented colonies of *Larus ribidundus* in the marshy area, the food composition of *C.p.* (numerous songbirds and other prey of open fields) indicated that this species had been mostly hunting outside the marshy area in meadows and crops.

Northern France.

The only conclusions on habitat selection refer to *C.a.*, whose food composition during the nesting period indicated that these birds had been mainly hunting in marshes and open fields. Typically marsh inhabiting species included *Gallinula chloropus* and *Rallus aquaticus* but an additional *Crex crex* was probably caught in damp meadow or grassy fields. On most occasions more prey species from open field were supplied by males than by females.

Southern France.

Of *C.a.* mainly aquatic species were observed (fish, frogs, snakes, young Rallidae). The additional rabbits may have been taken from drier sites, like Sealavender sward and edges.
In winter *C.a.* preyed mainly upon Anatidae, apparently in the open marshes where ducks were abundant.

Comparison.

In all of the study areas most of the prey items of *C.a.* must have been captured in marshy lands, but in Ameland, Terschelling, Flevoland

and Northern France additional prey species had been captured in the grasslands and Boschplaat (Terschelling), and in the open agricultural fields (Flevoland and Northern France).

Judged from the prey supplied to their nestlings, C.*c*. and C.*p*. must have been hunting in dunes and marshes. However there was evidence that both species more frequently hunted over meadows, Boschplaat and agricultural fields than did C.*a*.; C.*p*. apparently was relatively more active in these habitats than C.*c*.

During the two winter seasons in Flevoland C.*c*. exhibited its possibility to change from mainly hunting over open fields (after voles) to more hunting over marshes (after birds).

At least in the breeding season all three harrier species often hunted in the same habitats. In order to find out if quantitative differences exist in the use of these habitats, the following habitat distinctions have been made :

a. Breeding habitats, often with dense and rather tall shrub, scrub and bush herb vegetation in marshy areas and dunes

b. The surrounding fields, generally with lower vegetation : meadows, grasslands, saltings and agricultural fields.

The average use of these two types of habitat by the three harrier species is schematically indicated in Figure 3; C.*a*. showed a tendency to frequent marshes and dunes more than did C.*c*. and C.*p*., while C.*p*. frequented fields and grasslands more than did either C.*c*. and C.*a*. In C.*c*. and C.*p*. food observations gave evidence that the females more often hunted in the vicinity of the nest and consequently over a more structured vegetation than did the males. In C.*a*. males also supplied more field inhabiting prey than did the females.

These general conclusions concerning habitat preference concur with field observations at hunting harriers (Schipper, in prep.).

9. FACTORS INFLUENCING INTERSPECIFIC AND INTRASPECIFIC DIFFERENCES IN PREY SUPPLY AND PREY SELECTION.

9.1. Quantitative differences.

In the preceeding chapters interspecific and intraspecific differences and overlaps in food composition were recorded. However nothing so far has been said about the real food demand expressed in prey numbers in a given period of time and also about the factors influencing prey selection.

In relation to the prey numbers required, quantitative interspecific differences appeared to be present in harriers, whereas in relation to the prey selection some factors were found to induce qualitative differences and overlap in food composition. Some factors probably influence quantitative as well as qualitative differences. This section will deal mainly with the factors that induce quantitative differences.

9.1.1. *Number of prey items required.*

The number of prey items required was summarized for the periods that the young in the nests were fed by the parents. Although the adult birds shared in the food supplied we got the impression that generally the number of young to survive was ultimately related to the number of prey items supplied. This means that in some cases one or more young died, until the amount of food supplied was sufficient for the remaining number of young. This conclusion does not concur with those of Tinbergen (1940) in *Falco tinnunculus*, Luttich et *al.* (1970) in *Buteo jamaicensis* and of de Vries (1973) in *Buteo galapagoensis*. However, Lack (1966) discussed the dependence of breeding success on prey densities in other species.

The number of prey items was calculated for a period of 100 hours of nest observations and per single young. This was done by dividing the total number of prey items observed at a certain nest by the number

Table 18: Number of prey items, supplied by adults per 100 hours of nest observations and per young. Mean, standard deviation, number of nests and 95 % confidence limits of the mean are shown. Not included: *C.a.* in Northern France because of exceptional circumstances explained in Chapter 6.2.

Locality	*C. pygargus*	*C. cyaneus*	*C. aeruginosus*
Ameland			
mean ± s.d.	31.4 ± 9.8	24.7 ± 6.4	10.0 ± —
n	5	9	1
c.l.	19.2, 43.6	17.3, 32.1	—
Terschelling			
mean ± s.d.	44.4 ± 23.9	17.2 ± 4.3	12.0 ± —
n	6	9	1
c.l.	19.4, 69.4	13.9, 20.5	—
Flevoland			
mean ± s.d.	27.0 ± 5.7	25.0 ± 7.1	20.5 ± 6.3
n	2	2	2
c.l.	— 24.3, 88.3	— 39.0, 89.0	— 36.3, 77.3
Groote Peel			
mean ± s.d.	54.0 ± —	—	—
n	1	0	0
c.l.	—	—	—
Southern France			
mean ± s.d.	50.5 ± 28.3	—	19.0 ± 1.4
n	2	0	2
c.l.	—205.5, 306.5	—	6.4, 31.6
Overall			
mean ± s.d.	39.6 ± 19.6	21.3 ± 7.0	16.8 ± 5.5
n	16	20	6
c.l.	28.8, 50.4	18.0, 24.6	11.0, 22.6

of observation hours and the number of young, and multiplying the result by 100. Mean values obtained in this way are presented in Table 18. In general *C.a.* exhibited a relatively low number of prey items per young, *C.p.* the highest number.

In contrast to the preceeding chapters in which only the relative food composition has been considered, we now have to take into account the quantitative differences in food supply, in order to be able to compare the food demand in a given period per single young. This has been done for the three study areas in which direct interspecific comparisons were made.

Table 19: Comparison of prey selection and prey requirement (in numbers) per 100 hours of nest observations and per young.

Prey category	Ameland			Terschelling			Flevoland 1971		
	C.p.	*C.c.*	*C.a.*	*C.p.*	*C.c.*	*C.a.*	*C.p.*	*C.c.*	*C.a.*
Limicoles pulli	1.5	4.3	0	1.0	0.8	3.1	2.1	1.1	0
Pheasants	1.9	3.3	1.0	0	0.5	0	2.1	2.2	10.4
Passeriformes, pulli and Starlings not included	10.5	7.6	0	14.9	9.7	0.3	6.6	5.2	1.9
Passeriformes pulli	2.6	0	0	3.7	0	0.3	11.5	1.1	1.1
Voles	7.2	1.4	0	0	0	0	2.9	6.9	0.8
Rabbits	0.7	3.7	4.8	0.1	4.0	6.2	1.5	1.5	2.7
Other and unknown prey	7.0	4.4	4.2	24.7	2.2	2.1	0.3	7.0	4.1
Total (see Table 18)	31.4	24.7	10.0	44.4	17.2	12.0	27.0	25.0	21.0

Numbers obtained in this way (Table 19) again showed the same prey categories as in Chapter 6.2. to be the most important. The greatest overlap apparently occurred in the total predation on Passeriformes by *C.c.* and *C.p.* and in the predation of rabbits by *C.a.* and *C.c.*

These data do not yet tell anything about differences in the participation of males and females in supplying prey to their young. During the nestling period the ratio of prey numbers taken by males and females was generally not constant, but it was impossible to take any changes in participation by males and females during the nestling period into account. See Chapter 9.1.2.

It was shown in Table 19 that in one species the number of prey items required per young was not the same in each of the study areas.

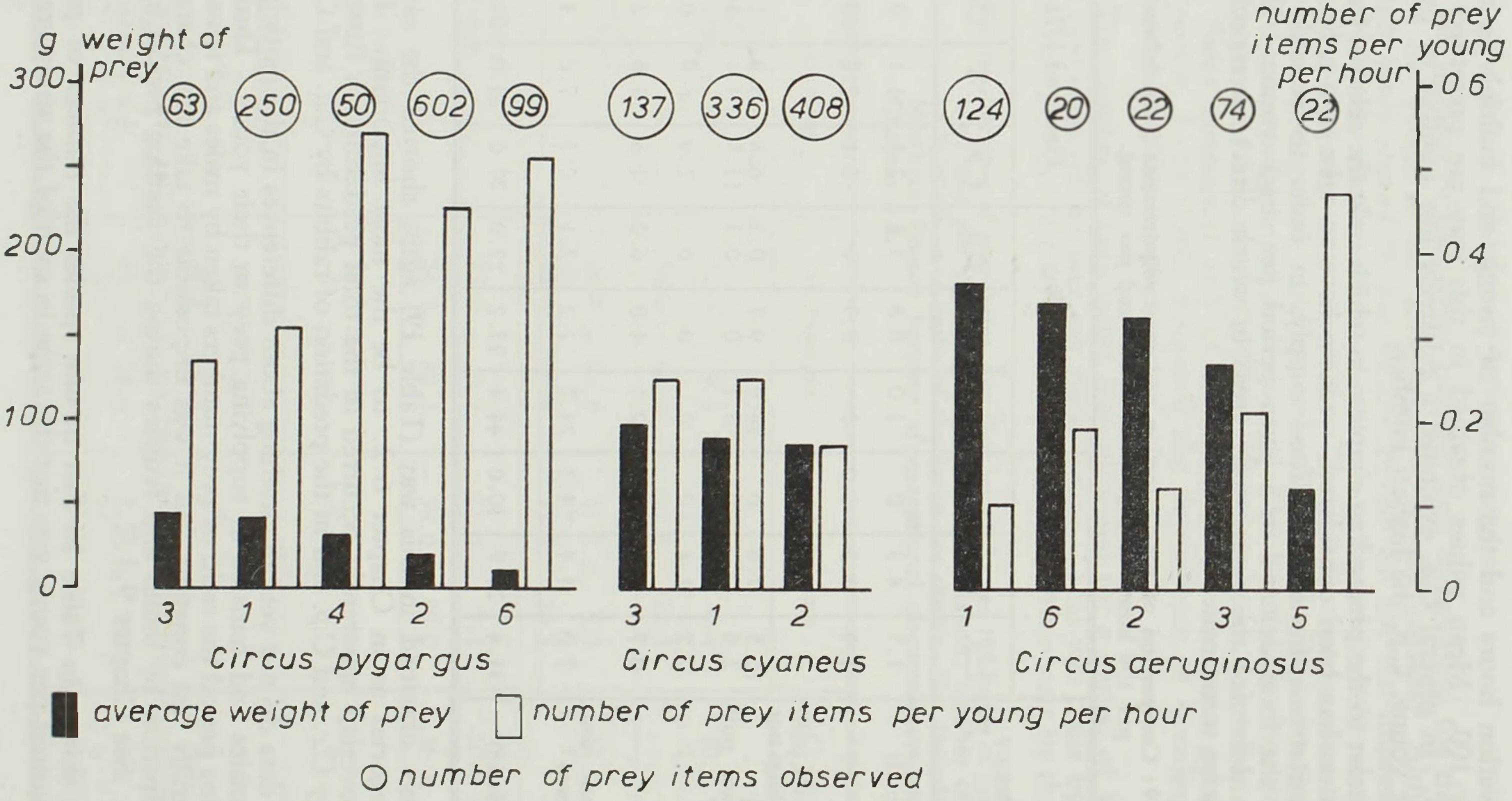


Fig. 4. — Comparison of average weight of prey and number of prey items in different study areas.
1 = Ameland; 2 = Terschelling; 3 = Flevoland; 4 = Groote Peel; 5 = Northern France; 6 = Southern France.

Probably this number was ultimately related to the selection of certain prey species or categories. In localities where small prey items were supplied prey numbers were mostly high and vice versa (see Figure 4). For inter- and intraspecific differences in prey weight, see Chapter 9.2.5.

In *C.a.* the prey numbers per hour were comparatively high in the Camargue. It is not conclusive whether this feature can be completely explained by the shorter period of daylight in Southern France as compared with the other localities studied, or by the limited food value of some prey categories. Snakes in particular were poorly exploited and many remains were left around the nests.

The extreme values in Northern France should be noted.

In *C.c.* the prey numbers supplied were not very different in the three study areas which corresponds to similar average prey weights.

In *C.p.* the prey numbers were comparatively high in Groote Peel. In this area some eggs did not hatch, possibly because of biocide poisoning (Koeman, pers. comm.). Therefore this additional factor as well as the food supply determined the ultimate number of young fledged.

It will be clear that in cases of interspecific overlap in food composition, overlaps in the categories of heavy and small prey, as a rule, are of different significance, as in cases of large prey items a smaller number is required in relation to the smaller prey items.

In Figure 4 prey weights are shown. Only the weights of complete prey animals are included as it was impossible to indicate what proportion of the total prey was actually eaten and what was discarded.

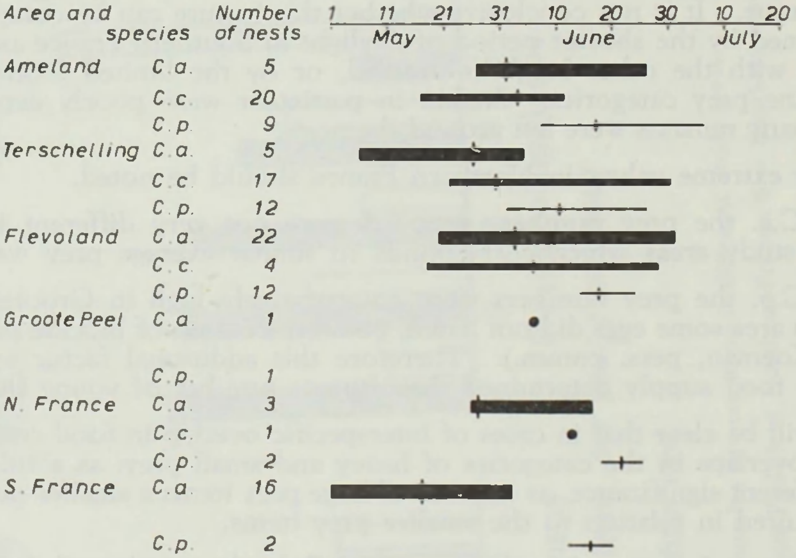
In the calculations all prey items observed are considered to have been fed to the young. However as mentioned above, there is evidence that the adult male and female frequently share in the eating of the prey. It is possible that all of the prey captured is supplied to the nest and that the adults take their share from this prey.

9.1.2. *Breeding time and development of young.*

It is a well known fact that the European harrier species do not breed at the same time of year. As a consequence, the period of maximum food requirement for the young of each species is dispersed throughout the common breeding season. In Figure 5 these periods are depicted by comparing the hatching date of the first egg observed during our study years (in Flevoland the year 1972 is also included and in Southern France some years prior to 1969).

It is shown that within large ranges the median values per species are only slightly different, especially in *C.a.* and *C.c.*, but in each locality the interspecific differences are apparent, *C.a.* being the earliest breeder, *C.p.* the latest. As the incubation period of *C.a.* is a few days longer than in *C.c.*, the median date of the first egg will be even earlier.

It may be noted that in our study areas the longest daylength is on June 21-22. At that time, when possibilities for large daily food supplies are optimal, the young of *C.p.* as a rule are small, whereas those of *C.a.* and *C.c.* are in a further stage of development.



— Fig. 5. Hatching dates of first egg : Median value and range.

In Chapter 9.1.1. attention has been drawn to the specific differences in food requirement per nestling. Important overlaps in prey composition appeared to be present. Considering the significance of

Table 20 : Number of prey items supplied by males and females together in different periods after hatching of the first egg. m = mean number of prey items per 100 hours of observations and per young ; r = range ; n = number of nests observed.

Species		Number of days after hatching of first egg		
		1-10	11-20	21 and more
Circus pygargus	m	26	39	43
	r	12-43	22-91	18-75
	n	6	13	14
Circus cyaneus	m	24	17	26
	r	12-29	5-23	13-33
	n	6	16	16
Circus aeruginosus	m	20	17	18
	r	12-28	8-24	11-24
	n	2	4	6

Table 21 : **Number of prey items supplied by males and females in different periods after hatching of first egg. Each horizontal row of figures represents data from a separate nest. § = see remarks in text.**

Locality and species	Number of days after hatching					
	1-10		11-20		21 and more	
	♂	♀	♂	♀	♂	♀
Circus aeruginosus						
Flevoland	—	—	4	2	12	3
Southern France §	4	0	22	5	18	3
Total	4	0	26	7	30	6
Circus cyaneus						
Ameland	—	—	2	3	26	21
	—	—	14	6	23	24
	—	—	7	1	8	17
	—	—	14	28	3	8
	—	—	—	—	1	16
Terschelling	3	2	0	3	—	—
	—	—	2	8	0	7
	—	—	1	0	1	7
	—	—	6	3	2	14
Flevoland	8	1	12	8	0	1
	—	—	12	1	14	7
	16	3	9	6	5	6
	—	—	—	—	10	8
Total	27	6	79	67	93	136
In %	82	18	54	46	41	59
Circus pygargus						
Ameland	—	—	14	17	26	42
	—	—	8	12	9	19
	2	1	33	7	21	1
	—	—	11	3	5	1
Terschelling	—	—	5	9	4	8
Flevoland	5	0	12	5	—	—
	—	—	30	8	—	—
Groote Peel	—	—	34	5	16	4
Southern France	—	—	—	—	9	4
	—	—	—	—	27	57
Total	7	1	147	66	117	136
In %	87	13	69	31	46	54
Average % C.c. and C.*p*.	85	15	62	38	44	56

these overlaps the specific differences in nestling periods referred to above are of importance. Observed overlap in the food composition of the three species of harrier is therefore divided in time as the nestling periods differ.

Tinbergen (1940) found in *Falco tinnunculus* that the prey supply frequency gradually increased until the nestlings were about three weeks old. In the present study it proved impossible to conclude that in any particular stage of development of the young, more prey was supplied than in other stage (Table 20). Study on this subject should be continued.

So far the degree of participation of males and females in total prey supply to the nests has not yet been discussed. In all three harrier species there was evidence that when the young are small, females often stayed on or near the nests and probably did not participate in obtaining the food. Later on, the females began to supply more and more food on their own. Simultaneously males appeared less often near the nests. In a number of cases the males seemed even to have disappeared by the time of fledging . These field impressions appeared to be confirmed by the data presented in Table 21, although in different nests of the same species, trends in this respect could differ. In *C.a.* the data of intraspecific differences are possibly biased, as the number of prey items of unknown origin (provided by male or female) is high. In this prey category the share of females is undoubtly higher than that of the males, so it is probable that the numbers of prey items taken by the males and females may show other real differences, and they are not included in the average values.

Assuming :

(*a*) that the total number of prey items per hour, supplied by males and females together, remained approximately the same throughout the nestling period;

(*b*) that the ratio of participation by males and females in prey supply in all three harrier species changes during the nestling period according to the average percentages of *C.p.* and *C.c.* in Table 21;

(*c*) that the data of first hatching in *C.a.* and *C.c.* show a difference of three days on the average, in *C.c.* and *C.p.* of twelve days; and

(*d*) that the food requirement of the parent birds are discounted (see Chapter 9.1.1.);

then the participation of males and females of all three species in food supply per young can be compared as in Figure 6. As the supply of food is continued during the weeks of the post-fledging period, the curves covering that period have been drawn by extrapolation. One has to keep in mind that in this way only medians and averages are involved, and that in any situation the deviations from these lines can be considerable.

The overlaps and differences in food composition, both interspecific and intraspecific, should be considered within the limits of simultaneous participation in the food supply of nest young by males and females of all harrier species present. According to Figure 6 the inter- and intraspecific relations are not constant in this respect; these overlaps and differences therefore need different interpretations at any given moment of the fledging and post-fledging period. Still, some general observations can be made.

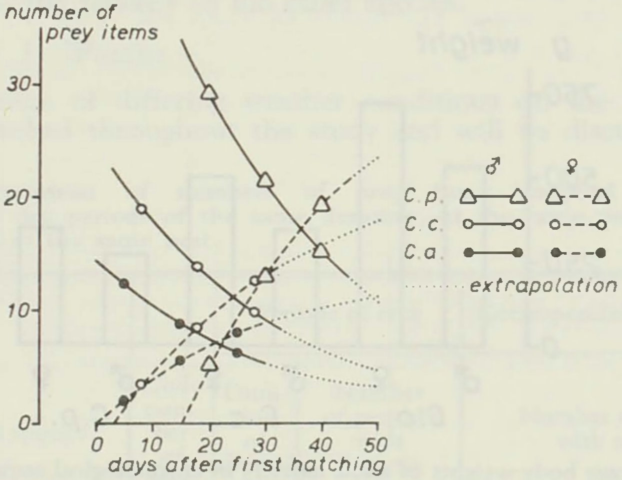


Fig. 6. — Comparison of prey numbers, supplied per 100 hours of nest observations and per young in Ameland, Terschelling and Flevoland.

As in the beginning of the nestling period males especially are more active in supplying food for the young and towards the end particularly the females, males and females of the different species will often hunt at the same time, whenever more than one species nest together. At the moment in the life cycle of *C.p.* when the maximum food is required and the *C.p.* males but not yet the females are most active, the females of *C.a.* and *C.c.* have started to be rather active, whereas the *C.a.* and *C.c.* males are gradually limiting their participation in the capture of prey.

If one unravels Figure 6 the following chronological sequence of importance of predation arises :

C.a. males - *C.a.* females - *C.c.* males - *C.c.* females - *C.p.* males - *C.p.* females. It should be noted that this sequence corresponds well with the sequence of body weight of the three harriers, *C.a.* being the largest, *C.p.* the smallest (Figure 7). This sequence is built up in such a way that chronologically, interspecific steps are greatest. When the real chronological interrelationships are incorporated in this model, the smallest steps in body weight are separated by the greatest span of time (*C.c.* male-*C.p.* male and *C.c.* female-*C.p.* female; see Figure 8).

The conclusion seems justified that a tendency is present, that at any time during the breeding season greater predation activity is displayed simultaneously by those harriers differing most strongly in size and therefore predation potential.

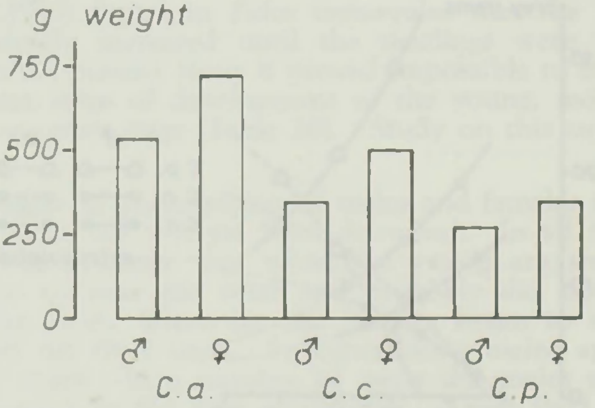


Fig. 7. — Average body weights of adult harriers in chronological sequence of greatest predation activity, unraveled in time during the breeding season (weight data derived from Nieboer, 1973).

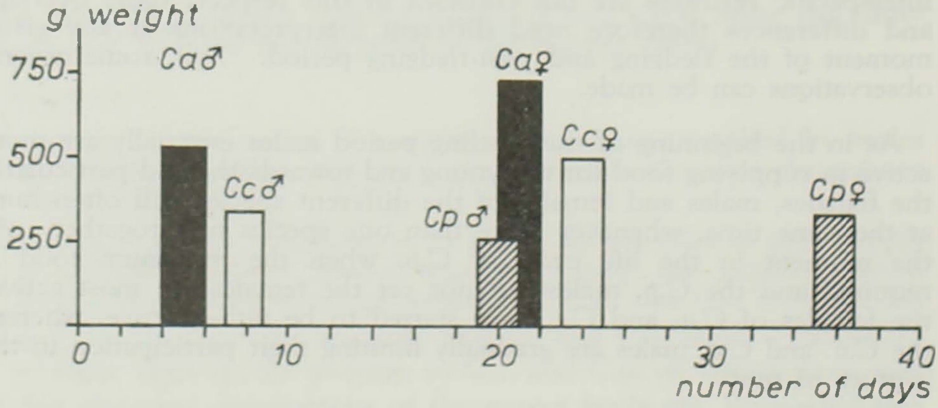


Fig. 8. — Average body weights of adult harriers in chronological sequence of greatest predation activity during the breeding time (weight data derived from Nieboer, 1973).

A similar situation may be present, for example, among sympatrically and symtopically living members of the genus *Accipiter*; in Europe *Accipiter gentilis*, the larger species, breeds before *A. nisus* (Opdam, 1972); in North America *A. gentilis* breeds before *A. cooperii* and *A. striatus*, whereas *A. striatus* is the latest breeder (Craighead and Craighead, 1956).

The sexual dimorphism in size in *C.p.* is among harrier species a relatively small one (Nieboer, 1973). In this context the isolated position of the *C.p.* female in Figure 8 is noteworthy, but increasing the body size would needlessly reduce the interspecific size differences in relation to the females of the other species.

9.1.3. *Weather.*

The influence of differing weather conditions on the prey supply has been checked throughout the study and will be discussed below.

Table 22: Comparison of numbers of prey items supplied during wet and dry periods of the same duration, at the same time of the day and at the same nest.

Locality and species	Code number of nest	Periods of rain			Corresponding dry periods			
		Duration of shower in hours	Number of periods with n preys		Number of periods with n preys			
			n = 0	n = 1	n = 0	n = 1	n = 2	n = 3
Circus aeruginosus								
Flevoland	13	0.50	1	—	2	2	—	—
	15	0.50	—	1	3	—	—	—
	15	1.25	1	—	1	2	—	—
Northern France . .	1	0.50	1	—	3	—	—	—
	1	0.50	1	—	2	—	—	—
	1	0.75	1	—	1	1	—	—
	1	0.50	1	—	2	—	—	—
Southern France . .	7	1.00	1	—	5	3	—	—
	7	1.00	1	—	2	4	2	—
	7	1.50	1	—	1	5	1	1
Circus cyaneus								
Flevoland	1	1.00	1	—	—	1	1	—
	D 7	1.00	1	—	—	2	1	—
Circus pygargus								
Flevoland	2	1.00	1	—	1	—	—	—
Groote Peel	3	1.50	1	—	2	2	2	2
	3	1.25	2	—	2	2	1	—
	3	1.25	1	—	1	2	—	—
	3	1.00	1	—	3	3	2	—
	3	0.50	1	—	5	3	—	—
	3	0.25	1	—	8	1	—	—

a. Rain.

Periods of rain during nest observations have been compared with corresponding periods on other days at the same nest during dry weather. Only rain with an intensity of at least 0.2. mm an hour was considered. The results are shown in Table 22.

Rain reduced the prey supply in all three harrier species. Generally no interspecific differences in prey supply resulting from rain could be established. On one occasion however, during a long sustained period of rain, C.c. supplied 16 prey items and *C.p.* none (Terschelling, 1961).

Table 23: Comparison of wind velocity and supply of small mammals and birds to the nest young during nest observations. Mean values of wind velocity in m/sec, standard deviation, number of prey items and 95 % confidence limits of the difference between the means are given.

Locality and year	Sex and individual code number of the bird	voles, mice	birds	c.l.
C. aeruginosus				
Flevoland 1971	♂ 15	13.7±8.0 (n = 6)	8.7±4.5 (n = 9)	—2.8–12.8
C. cyaneus				
Ameland 1967	♂ I	4.9±1.5 (n = 5)	6.4±2.2 (n = 23)	—3.2– 0.2
	♂ II	5.4±2.7 (n = 4)	5.1±1.5 (n = 21)	—2.6– 3.1
Flevoland 1971	♂ 1	7.8±2.8 (n = 4)	7.8±3.2 (n = 15)	—3.5– 3.4
	♂ 2	3.8±2.2 (n = 10)	5.1±2.9 (n = 14)	—3.5– 0.8
C. pygargus				
Ameland 1967	♂ I	7.2±3.3 (n = 13)	4.9±0.5 (n = 16)	0.1– 4.4
	♀ I	6.3±2.9 (n = 30)	5.4±1.6 (n = 9)	—0.6– 2.4
	♀ II	4.8±0.6 (n = 7)	7.6±3.0 (n = 16)	4.4– 1.1
Ameland 1970	♂ 10.4	4.6±2.9 (n = 4)	6.3±3.0 (n = 45)	—4.7– 1.4
Flevoland 1971	♂ 3	4.6±1.4 (n = 6)	5.9±1.9 (n = 25)	—2.7– 0.1

During dull or rainy weather *C.p.* brought lizards to their nests in Terschelling with a strikingly high frequency; the same applies to voles and mice in Ameland and Terschelling.

It is possible that this and other types of weather induce harriers to search for particular prey species and by doing so influence the interspecific differences in food composition.

b. Wind.

HENNINGS (1936) concluded from nest observations that during calm weather *C.c.* supplied more voles to the young and during windy periods more birds. Our data from Flevoland enabled us to check the general value of this conclusion (Table 23). In only a few cases the average wind velocities associated with supply of small mammals and of birds differed significantly, but the differences were not at all constant. As in Ameland wind measurements had to be taken from Vlieland; the comparisons in Flevoland are more reliable. Here *C.p.* and *C.c.* tended to supply birds at higher wind velocity, *C.a.* at lower wind velocity, but significant differences were not found. The observations should be complemented by nest observations covering longer periods at one nest.

In order to check the influence of wind velocity on hunting success prey numbers supplied during high and low wind velocity were compared (Table 24). Wind velocity was considered to be high if it exceeded 8.7 m/sec. On the average *C.p.* and *C.c.* tended to supply

Table 24: Comparison of prey numbers supplied during periods of nest observations with high and low wind velocity of the same duration, at the same time of the day and at the same nest.

Locality and species	Code number of nest	Duration of period in hours	Number of periods		Average prey numbers per hour	
			Wind velocity		Wind velocity	
			High	Low	High	Low
Circus aeruginosus						
Flevoland	13	1.5	1	4	1.3	0.8
	13	1.0	2	3	1.0	0.7
	13	3.5	2	2	0.9	1.0
	15	2.0	2	2	0	0.8
	15	1.0	1	3	0	1.7
	15	1.0	2	2	0	0
	15	1.0	2	2	1.0	0.5
	15	3.5	1	3	0.6	0.3

(Table 24 : continuation)

Locality and species	Code number of nest	Duration of period in hours	Number of periods		Average prey numbers per hour	
			Wind velocity		Wind velocity	
			High	Low	High	Low
Southern France . .	7	1.5	1	8	0.7	0.8
	7	5.0	1	6	0.8	0.8
	7	2.0	2	6	0.5	0.7
	5	9.0	1	4	0.3	1.1
Ameland	1	1.0	1	5	1.0	0
	1	1.0	1	3	0	1.0
	1	3.0	1	3	0.7	0.3
Mean	—	—	—	—	0.6	0.4
95 % conf. limits of diff. between means . . .	—	—	—	—	— 0.3,	0.7
Circus cyaneus						
Ameland	2	2.0	1	7	0	0.4
	2	1.0	3	6	0.3	0.5
	2	2.0	3	6	0.8	0.2
	2	1.0	2	7	0.5	0.3
	2	1.0	1	8	0	0.3
	I	6.0	1	4	0.8	0.5
	I	4.0	1	4	1.8	1.1
	IV	14.0	1	4	0.8	0.5
	10,8	2,0	1	3	0.5	0.7
	10,8	1.0	1	3	0.0	1.0
	10,8	5.0	1	3	0.6	0.6
Flevoland	1	1.0	1	3	0	1.0
	1	1.0	2	2	0.5	0.5
	1	1.0	2	1	0.5	0
	1	2.0	2	2	1.0	0.5
	1	1.0	3	1	1.0	0
	I	1.0	2	2	1.5	0
	1	1.0	1	2	0	0.5
	3	1.5	1	4	2.0	0.5
	3	1.5	1	3	0.7	0.7
Mean	—	—	—	—	— 0.7	— 0.5
95 % conf. limits of diff. between means . . .	—	—	—	—	— 0.1,	— 0.5

(*Table 24 : continuation*)

Locality and species	Code number of nest	Duration of period in hours	Number of periods		Average prey numbers per hour	
			Wind velocity		Wind velocity	
			High	Low	High	Low
Circus pygargus						
Ameland	1	1.0	1	6	2.0	0.8
	1	1.0	2	6	0.5	0.5
	1	1.0	4	5	0.5	0.8
	1	1.0	5	4	0.8	1.8
	1	1.0	3	6	0	0.3
	1	1.0	3	6	0	0.5
	1	2.5	2	5	1.2	0.6
	1	1.0	1	5	2.0	0.6
	10.4	7.5	1	5	0.7	0.7
	10.4	1.0	2	5	1.0	0.8
	10.4	6.0	1	6	0.3	0.6
	I	1.0	1	4	0	2.5
	I	3.0	2	3	1.7	1.1
	I	2.0	1	4	4.5	1.1
	II	7.5	1	4	0.9	0.5
	II	5.0	1	1	0.6	0.7
Flevoland	2	3.5	1	3	0	1.0
	3	1.0	1	5	0	0.6
	3	2.0	1	4	0.5	0.6
	3	1.0	1	0	1.0	0
	3	1.0	1	4	0	1.0
Mean	—	—	—	—	0.9	0.8
95 % conf. limits of diff. between means . . .	—	—	—	—	— 0.4,	— 0.6

more prey items at high wind velocity, *C.a.* at low wind velocity. The differences between the prey numbers at high and low wind velocity were not significant in any of the harrier species, although most nearly significant in *C.c.* An eventual increase of hunting success at high wind velocities would be of particular interest in comparison to the presumed increase of hunting success on birds during periods of high wind velocity, discussed above. The observations did not show that *C.p.* is particularly favoured by higher wind velocity, as Nieboer, (1973) suggested, in calling *C.p.* an ‚adverse wind hunting specialist'.

With regard to the way in which strong winds might exert their influence on hunting success, the following possibilities will be checked in the chapter on hunting behaviour :

(*a*) Hunting harriers may exploit high wind velocities for acceleration, for sudden changes in their flying direction and speed when first sighting prey, for hovering, poising or maintaining a slow airspeed;

(*b*) Hunting harriers may be hindered in sighting prey because of moving vegetation, especially if the vegetation is tall, although when the bird is hunting against the wind, the visibility into the vegetation may increase;

(*c*) Strong winds might influence the activity and therefore the accessibility of prey species.

c. Temperature.

In trying to study the influence of temperature differences on the prey supply one meets with the difficulty that changes in temperature often coincide with other environmental changes. Highest temperatures of the day usually occur after midday and rain usually lowers air temperature.

In Chapter 9.2.3. the significance of daily rhythm is discussed. It is stated that in the Camargue most snakes were supplied by *C.a.* during midday, when temperatures were 18° C or more. However one day when the temperature did not rise above 18° *C.a.* still took snakes during midday, so that the daily activity pattern of the snakes was probably the relevant factor in this case. It has also been mentioned that rainy or dull weather favoured the supply of lizards by *C.p.* Apparently lower temperatures reduced the activity of the lizards and hence made them more vulnerable.

Of particular interest is the average prey weight supplied per hour and per young by *C.p.* in Southern France, which is strikingly low in comparison with the other areas (See Table 25). Although raptors in general need less food at high temperatures (Craighead and Craighead, 1956; Brown and Amadon, 1968) and during the observation periods in Southern France the temperatures were very high in relation to the other areas, this cannot fully explain the differences mentioned.

Table 25 : *Circus pygargus,* **average prey weight supplied per hour and per young during nest observations** (see also Fig. 4).

Locality	Weight (g)
Ameland	12.9
Terschelling	9.0
Flevoland	11.3
Groote Peel	16.8
Southern France	5.7

As hot weather generally lowers the food requirement, those species of harrier nesting later in the year will probably require, on the average, relatively less food in relation to their body weight than the earlier breeders. This could be the reason why, in relation to its body weight *C.a.* requires more prey weight per hour and per young than C.c. and *C.p.*, and *C.p.* less than both *C.c.* and *C.a.* However data on this subject, summarized in Table 26, does not fully confirm this hypothesis. It is probable that the food value of the various prey species should have been incorporated in this comparison.

Table 26: Comparison of average prey weight (g) supplied during nest observations per hour, per young and per harrier species in Ameland, Terschelling and Flevoland.

	C.*p*.	C.*c*.	C.*a*.
(a) Average prey weight per hour per young	10.8	19.9	21.8
(b) Average weight of harrier species	305	420	625
Ratio (a)/(b) × 1.000 . . .	35	47	35

9.2. Qualitative differences.

9.2.1. *Prey densities and individual variation.*

Density of prey populations form the primary factors in the process of prey selection. Since in no two areas are prey densities exactly the same it is very difficult to obtain an average picture of the specific characteristics of the prey selection of harriers.

Fluctuations of prey densities will be reflected in the food composition of all three harrier species, but these changes will not necessarily be the same in all three species. Differences in prey densities will therefore either enlarge or reduce inter- and intraspecific overlaps in prey selection. In addition individual variation in characteristics of prey selection has to be taken into account. We noticed that at the same time and on the same place even harriers of the same species and sex exhibited different choice of prey. Part of this feature may have been induced by individual degrees of specialization on particular common prey species, as recorded in other birds of prey (Brüll, 1964), that results in reducing intraspecific competition.

Our data on the individual results of predation and therefore of individual prey preference, are limited, but those that are available have been summarized in Table 27.

Table 27: Comparison of food compositions of different individuals in both sexes of three harrier species (see sign beside sex symbols), in the same area and corresponding periods of the breeding season; from nest observations.

Prey category	C. *pygargus*						C. *cyaneus*						C.*a.*	
	Ameland 1967				Flevoland 1971		Ameland 1967						S. France 1969	
	♂$_1$	♂$_2$	♀$_1$	♀$_2$	♂$_2$	♂$_3$	♂$_1$	♂$_2$	♀$_1$	♀$_2$	♀$_3$	♀$_4$	♂$_5$	♂$_7$
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—	—	—	6	2
3	—	—	—	—	—	—	—	—	—	—	—	—	—	2
4	—	—	—	—	—	—	—	—	—	—	—	—	24	43
5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	3	—	—	6	10	12	2
7	—	18	—	—	—	—	4	—	13	—	11	15	6	2
8	3	—	2	6	13	3	11	16	17	3	28	34	12	—
9	38	53	12	32	50	49	64	35	54	27	33	24	18	12
10	33	6	54	23	25	24	21	14	—	13	6	7	6	7
11	—	—	—	6	6	18	—	11	17	43	—	24	12	29
12	—	—	—	—	—	6	—	—	—	—	—	—	—	—
13	28	24	32	19	6	—	—	22	—	13	17	2	6	—
n =	40	17	59	31	16	33	28	37	24	30	18	41	17	42

The influence of different prey densities will be illustrated by comparing food compositions of different years and in different areas, respectively.

a. Annual variation in food composition.

Differences in food composition in the same area but in different years have been studied in Flevoland, where the prey supply to the nest by two pairs of C.c. has been recorded in 1971 and 1972. In both years at least the same females (♀^{1} and ♀^{2}) were involved, so that individual differences were ruled out. Densities of available prey were rather different in these two years, pheasants (cat. 8) being more numerous, but voles (cat. 10) less so in 1972 than in 1971. The changed circumstances were fairly well reflected in the food composition (Table 28).

Table 28: Comparison of food compositions of *C.c.* in Flevoland in different years; from nest observations.

Prey category	♂$_1$ 1971	♂$_1$ 1972	♂$_2$ 1971	♂$_2$ 1972	♀$_1$ 1971	♀$_1$ 1972	♀$_2$ 1971	♀$_2$ 1972
6	—	—	—	—	—	—	—	13
7	—	—	—	—	—	—	9	—
8	21	93	4	10	22	40	9	63
9	58	3	52	80	22	27	55	25
10	21	—	40	—	33	—	18	—
11	—	—	—	—	22	33	—	—
12	—	—	—	—	—	—	—	—
13	—	3	4	10	—	—	9	—
n =	19	30	25	10	9	15	11	8

We have indications that in 1972 *C.a.* took also many pheasants. So competition between *C.a.* and *C.c.* increased unless in 1972 pheasants had to be considered as super-abundant prey species.

See also discussions on the annual variation in food composition of *C.c.* in winter (Chapter 7.2.).

b. Local variation in food composition (Table 6).

In the neighbouring islands of Ameland and Terschelling and also in Flevoland harriers nest abundantly. But there are noteworthy differences in the composition of the fauna of prey species, which are reflected in the food composition of the harriers. The differences in prey fauna concern particularly voles and lizards (Table 29).

Table 29: Presence of voles and lizards in some study areas.

Locality	Voles	Lizards
Ameland	+	—
Terschelling	—	+
Flevoland	+	—

In Ameland voles are numerous, but lizards are absent. Hence the food of *C.p.* included, apart from a large amount of small song birds, also numbers of voles. In the food of *C.c.* small songbirds, rabbits and young nidifugous land birds predominated, and voles and other prey categories were taken to a lesser degree.

In Terschelling lizards do occur but voles are absent. Young nidifugous land birds, especially pheasants, were less numerous than in Ameland. Hence *C.p.* supplied their young with Passeriformes and lizards; in contrast lizards were almost neglected by *C.c.* Instead *C.c.* took relatively more Passeriforme birds and more rabbits than in Ameland.

In Flevoland (1971) no lizards occur; but in 1971 pheasants and voles were rather numerous. The prey abundance therefore was more or less comparable to that in Ameland, although voles and pheasants were relatively more numerous. In this case *C.p.* and *C.c.* took a high percentage of Passeriforme birds, whereas *C.c.* supplied more voles than did *C.p.*

It is evident that depending on densities of other prey species, the occurrence of lizards is apt to reduce the overlap in prey selection of *C.c.* and *C.p.*

In Table 6 the prey selection of *C.a.* in Flevoland and in Southern France can be compared. A striking difference is found in the high percentage of aquatic animals taken in Southern France (cat. 2, 3, 4, 6). In the part of Flevoland where harriers were studied most of these prey species were less common or lacking, while pheasants were abundant and consequently frequently taken by *C.a.*

Note the differences in prey composition of *C.c.*, observed in winter in areas rich in voles, and also in Terschelling (Chapter 7.2.).

9.2.2. *Breeding time.*

Interspecific differences in breeding time have been discussed in Chapter 9.1.2. Here the possible effect of prey densities in the course of the breeding season on the qualitative food composition of the harriers will be discussed. The relatively early breeding time of *C.a.* and *C.c.* enables the birds to catch more young rabbits than later in the season when the number of young rabbits suitable for prey has diminished.

In Flevoland in 1971 most pheasant chicks were hatched in the second half of May (Van Zelm, pers. comm.). As most young of *C.a.* and *C.c.* hatched at the same time or somewhat later, pheasant chicks were available for them. As *C.a.*, on average, nested a few days earlier than *C.c.* the situation probably was most advantageous to *C.a.* In addition the larger size of *C.a.* must have enabled it to take also more of the larger chicks, but the latter feature could not be verified significantly in relation to *C.c.* (Chapter 6.2.).

During the nestling time of *C.a.* and *C.c.* young Limicolae and nidifugous water birds are also particularly numerous. *C.p.*, breeding later in spring, misses this great supply of young water birds, Limicolae, pheasants and alike. Therefore, more than *C.c.*, *C.p.* is forced to exploit another rich seasonal source of food, viz. Passeriforme birds, as well as voles, the latter having become more and more abundant in the course of late spring and early summer. As the summer advances, *C.p.* is in a more advantageous position to take large insects and lizards in areas where these prey categories occur. In Terschelling 1959, 1961 and 1962 for instance, it was recorded that in the course of the nestling period *C.p.* supplied increasingly more lizards (Table 30). The low percentages of lizards recorded here in 1959 (nest III) are probably due to the small number of observation hours during the part of the day that most of the lizards were usually caught.

Table 30: Percentage of lizards in the food of *C.pygargus*, Terschelling; from nest observations. Dash means: no observations.

Period	Year and code number of nest				
	1959		1961	1962	
	I	III	I	III	IV
June 10 - June 19	—	—	13	—	—
June 20 - June 29	21	—	72	11	—
June 30 - July 9	59	—	52	46	67
July 10 - July 19	—	0	—	67	68
July 20 - July 30	—	21	—	—	—

With respect to large insects as nestling food of *C.p.* it may be remarked that young in the nest observed in Southern France in the first week of July 1969 did not get large insects, but young of a second nest observed a week later received large numbers. Later visits to the first nest revealed prey remnants of large insects there also. Apparently *C.p.* adjusted its prey selection to the seasonal development of the insect fauna.

9.2.3. *Daily rhythm.*

Daily activity in harrier predation has been studied on the basis of prey supply to the nests. In Fig. 9 the prey supply per two hours of nest observations is shown for the three species of harriers and for all study years and areas combined.

It is clear that daily rhythms differ considerably (between species, years and study areas). Although males and females sometimes proved to have differing daily rhythms, these differences cannot explain the very different pictures, as for example in *C.p.*

It has to be noted that daily rhythm may bias, to a greater or lesser extent, the data on average prey supply to the young per 100 hours of observations in Chapter 9.1.1.

In *C.a.* the prey supply was highest during the middle part of the day in Ameland, Terschelling and Flevoland. In Camargue prey supply was almost constant throughout the day. (Pinowski, 1961, recorded an activity pattern of *C.a.* in Poland, where most prey items were brought to the nests in the morning with fewer during the second half of the day).

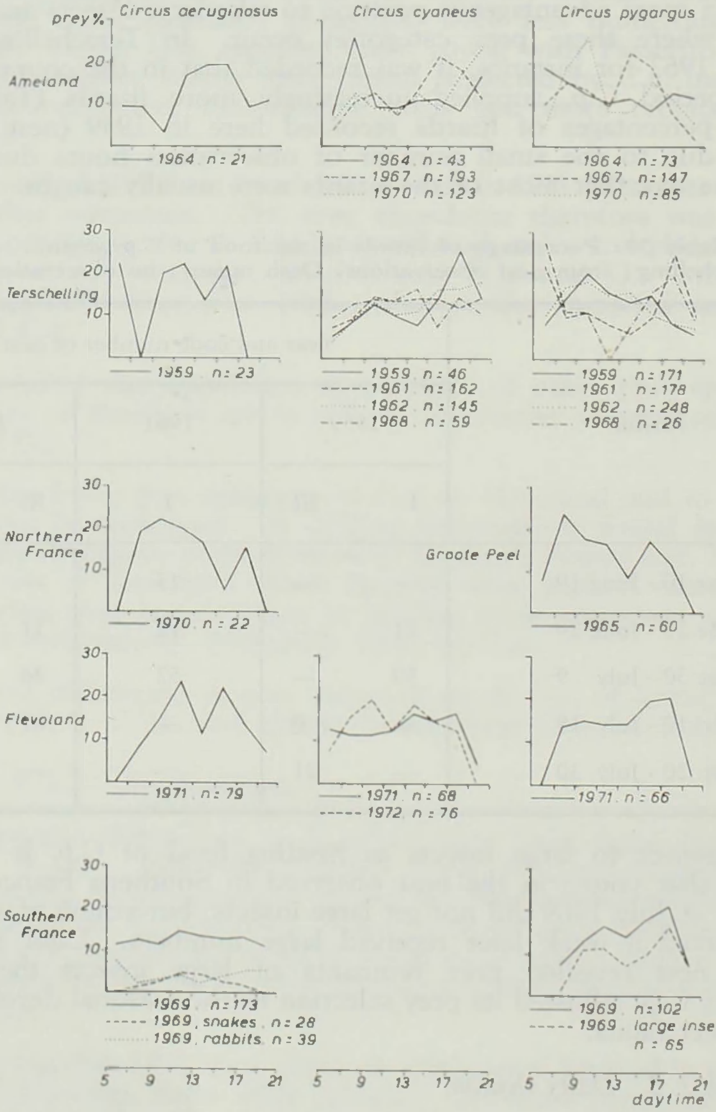


Fig. 9. — Daily rhythm in prey supply, summarized per 2 hours of nest observations (males and females combined).

In *C.c.* a slight regularity was present in Ameland and Terschelling, suggesting a slight and more or less gradual increase in activity in the course of the day. In 1964, however, C.c. showed a peak in the first part of the morning, whereas in 1967, two more or less pronounced peaks were present. In Flevoland C.c. showed a more C.*a*.-like pattern, with reduced activity in the last two-hour periods.

In C.*p*. the activity sometimes tended to decrease in the course of the day (Ameland 1964 and 1970, Terschelling 1959 and 1962, Groote Peel 1965). Activity patterns were similar in Terschelling 1959 and 1962, and different in 1961 and 1968. In 1959 and 1962 activity was maximum about midday, in 1961 and 1968 activity was minimum at that time.

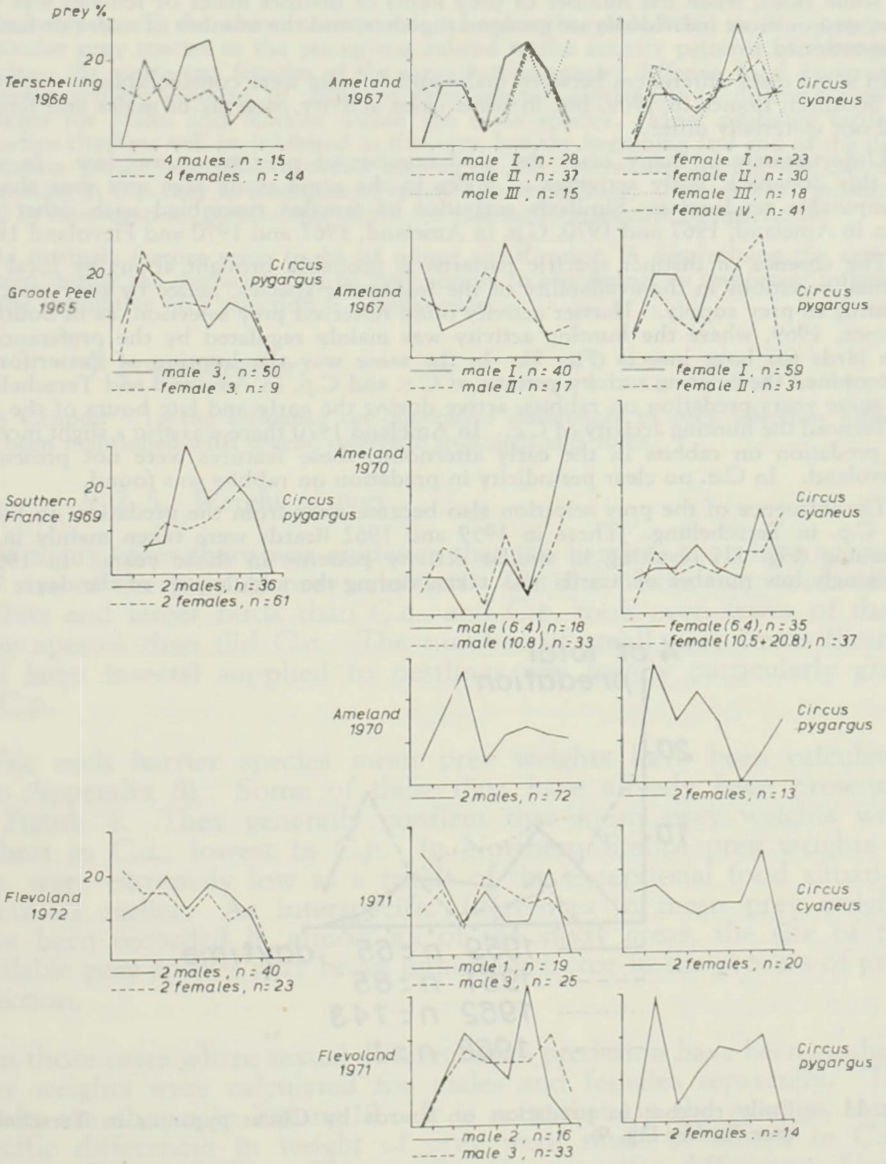


Fig. 10. — Comparison of daily rhythm of males and females. Example : «2 males»- prey of two males were included; «male 3» = male with code number 3. See further Fig. 9.

In several years, at different localities a span of relatively low activity in all harriers was observed during the period 11-15 hours : C.*a*. in 1959 and 1971, C.*c*. in 1959, 1962, 1964, 1967, 1970, and 1972, C.*p*. in 1961, 1965, 1967, 1968, 1969, 1970 and 1971. In many cases prey supply was low or not recorded in the first and last periods of the day. However C.c. occasionally displayed a considerable activity in the last period of the day, notably in Ameland 1970, where in this period Passeriformes were fed to the young. C.*p*., exhibited a great activity in the first two-hours period in Terschelling 1961 and 1968 and in Ameland 1964.

Fig. 10 gives a comparison of the daily activity of males and females when known. In some cases, when the number of prey items of distinct males or females was very low, two or more individuals are grouped together, and the number of males or females is mentioned.

In some cases differences between males and females were considerable, as with C.*p***.** in Southern France in 1969, but in some cases activity patterns of males and females did not materially differ.

Unfortunately in many cases the total number of prey items was low. In spite of this drawback, daily activities of males in the same study area and year showed comparable tendencies. Similarly activities of females resembled each other (e.g. C.c. in Ameland, 1967 and 1970, C.*p*. in Ameland, 1967 and 1970 and Flevoland 1971).

The absence of distinct specific patterns is probably brought about by local and annual variations in the availability of the main prey species, hence by prey selection relating to prey supply. Harrier activity often reflected prey selection, as in Southern France, 1969, where the hunting activity was mainly regulated by the preference of the birds for large insects (Fig. 9). In the same way the hunting of Passeriformes determined the hunting activity pattern of C.*c*. and C.*p*. in Ameland and Terschelling. In some years predation on rabbits, active during the early and late hours of the day, influenced the hunting activity of C.c. In Ameland 1970 there was also a slight increase in predation on rabbits in the early afternoon; these features were not present in Flevoland. In C.*a*. no clear periodicity in predation on rabbits was found.

The influence of the prey selection also became clear from the predation on lizards by C.*p*. in Terschelling. There in 1959 and 1962 lizards were taken mainly in the morning (Fig. 11) resulting in similar activity patterns in those years. In 1961 a strikingly low number of lizards was taken during the middle part of the day. This feature may be related to the time of the year and the weather. In 1961 the periodicity in predation on lizards was mainly determined by nest observations during the end of June; in 1959 mainly by observations during the last days of the relatively hot month

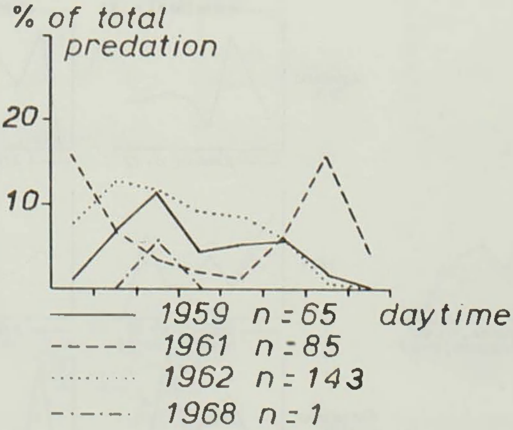


Fig. 11. — Daily rhythm in predation on lizards by *Circus pygargus* in Terschelling (See further Fig. 9).

of June and during the month of July, and in 1962 mainly by observations during July. In this respect circumstances in 1959 and 1962 were comparable and deviated from the situation in 1961. Only one lizard was among the 26 prey items observed in 1968; this may be due to the general decline of *Lacerta vivipara* in the area.

In Camargue, the most important prey categories of C.*a*. were rabbits and snakes (*Natrix sp*.). Predation activities on these species were more or less complementary as shown in Fig. 9. Fewer rabbits were taken during the daytime, when predation upon snakes became more apparent.

Probably in all the above mentioned examples the periodicity in the supply of particular prey species to the young was related to the activity patterns of these prey species. As males and females of the same harrier species differ in food preference, different activity patterns of different prey species may result in different activity patterns for males and females within the same species. Most probably intrinsic circadian rhythms will be inhibited in this way, but the beginning and end of the daily predation period and the recorded activity of C.c. increasing during the day and decreasing in C.*p*. may be examples of specific characteristics. Still, this is a promising field of investigation, particularly useful for making interspecific comparisons.

As intrinsic factors seem to be of minor signification in determining the activity pattern during the day according to prey supply to the young, an important influence on the qualitative prey selection is questionable.

9.2.4. *Weather.*

In Chapter 9.1.4.the influence on qualitative differences in prey selection already has been mentioned with special reference to lizards and voles.

9.2.5. *Weight of prey.*

In many cases there was evidence that the harriers took into account the size of the prey in prey selection. On the whole C.*a*. took more rabbits and larger birds than C.c., and C.*p*. took even fewer of these prey species than did C.c. The number of small prey items (lizards and large insects) supplied to nestlings was locally particularly great in C.*p*.

For each harrier species mean prey weights have been calculated (see Appendix 8). Some of these data have already been presented in Figure 4. They generally confirm that mean prey weights were highest in C.*a*., lowest in C.*p*. In Northern France prey weights in C.*a*. were extremely low as a result of the exceptional food situation discussed earlier. As interspecific differences in mean prey weights have been recorded in almost all of the study areas, the size of the available prey species may be an important factor in the process of prey selection.

In those cases where sexual differences in predation have been studied, prey weights were calculated for males and females separately. The results are shown in Figure 12. It is seen that on the average, intraspecific differences in weight of prey were small or absent in C.*p*., large in C.c. and C.*a*. The smallest interspecific differences found were those between C.*p*. females and C.c. males, and between C.c. females and C.*a*. males. See also Table 32 for inter- and intraspecific differences in prey size, obtained through additional field observations.

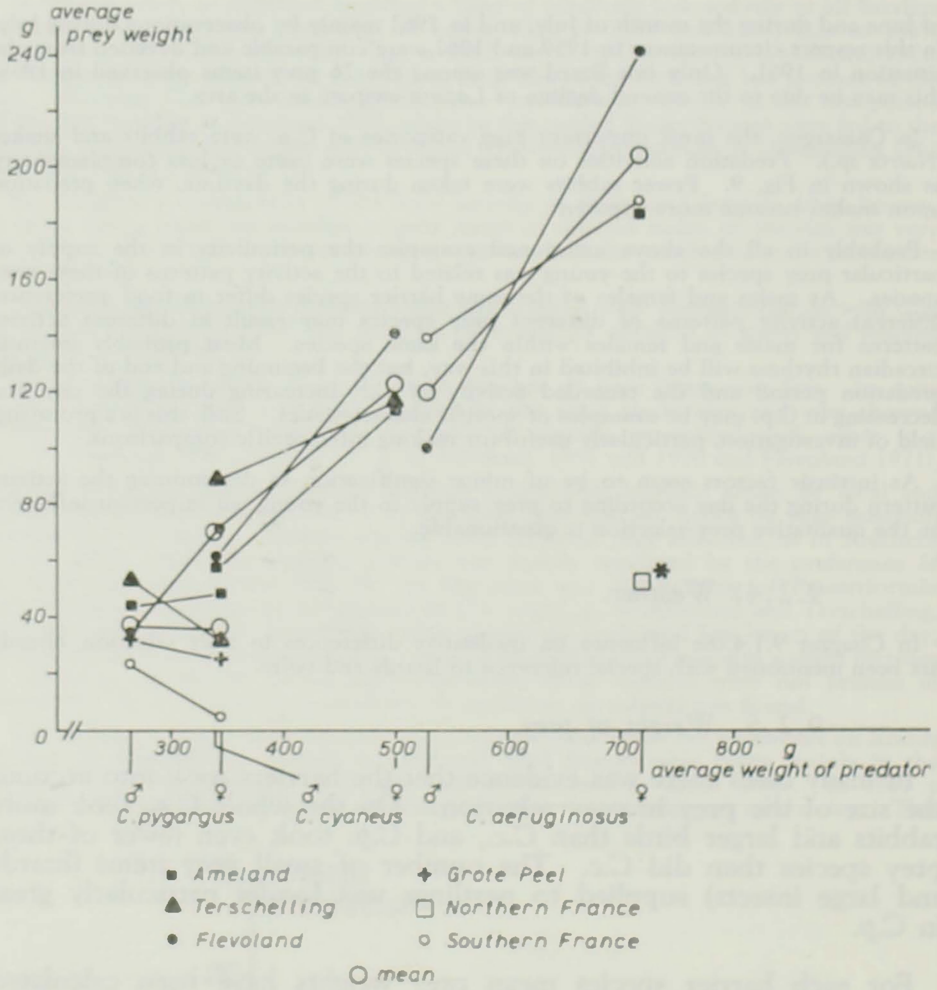


Fig. 12. — Relation of prey weight to weight of predator, male and female. Only prey, observed during nest observations, has been considered. See Table 31.

(*) Not included in mean because of exceptional circumstances explained in Chapter 6.1.

If measured by prey weight, inter- and intraspecific differences are smallest between *C.p.* males and females, between *C.p.* females and C.c. males, and between C.c. females and *C.a.* males. Hence overlap in prey composition, as far as prey selection depends on the prey size, may be largest in these categories. But the differences in breeding time and in period of main predation activity as discussed in Chapter 9.1.2. (Figure 8) must have a mitigating effect on eventual competition. Especially with respect to C.c. and *C.p.* with clearly differing breeding times, the tendency for separation C.c. males and *C.p.* females is evident.

The intra- and interspecific differences in average prey weight were not proportionately related to body size (weight) and often were larger

Table 31: Prey weight ranges and number of prey items, included in Figure 12.

Locality	Number of prey items and ranges of prey weight					
	C. *pygargus*		C. *cyaneus*		C. *aeruginosus*	
	♂	♀	♂	♀	♂	♀
Ameland	108 12-250	74 17-250	127 9-250	184 9-612	— —	20 25-300
Terschelling	9 17-100	17 17-100	15 25-250	44 20-250	— —	— —
Flevoland	47 17-250	13 17-250	81 10-500	42 20-500	30 10-675	10 30-675
Groote Peel	42 17-150	7 17-60	— —	— —	— —	— —
Northern France	—	—	—	—	—	20(*) 17-250
Southern France	34 1.5-60	60 1.5-29	— —	— —	58 17-425	14 20-425
Total	240 1.5-250	171 1.5-250	223 9-500	270 9-612	88 10-675	44 20-675

(*) Not included in total because of exceptional local circumstances discussed elsewhere.

Table 32: Size differences in prey, carried by harriers in the field in Flevoland, N. France and S. France.
«Small prey» includes mainly prey categories 1, 3, 5, 6, 9, 10, 13.
«Larger prey» includes mainly prey categories 2, 4, 7, 8, 11, 14.

Species	Number of prey items			
	♂		♀	
	small	larger	small	larger
C.*p*.	103	0	7	1
C.*c*.	21	2	5	2
C.*a*.	124	77	14	30
Total	248	79	26	33

than might be expected in relation to body size. These differences are correlated with foot size according to Nieboer (1973).

Table 33 presents data on the relation of prey weight to the weight of the harriers. *C.a.* males and females and *C.c.* females on the average supplied the heaviest, *C.p.* females the smallest prey items in relation to average body weight. Prey taken by *C.p.* males appeared to be of small size, also being much smaller than those taken by C.c. males. To really understand these results it will be appropriate to make some preliminary remarks on the hunting behaviour. Generally obvious inter- and intraspecific differences in behaviour were present if one compares the hunting distances, measured from the breeding area.

Table 33: Prey weights and body weights of harriers; the latter taken from Nieboer (1973). Only prey, observed during nest observations, has been considered.

	C. *pygargus*		C. *cyaneus*		C. *aeruginosus*	
	♂	♀	♂	♀	♂	♀
Number of prey items	240	171	223	270	88	44
Mean weight of prey	37.2	36.2	68.9	122.1	133.9	203.8
Mean weight of predator	265	345	340	500	530	720
$\frac{\text{Mean weight of prey}}{\text{Mean weight of predator}} \times 100$	14.0	10.5	20.2	24.4	22.3	28.3

C.a. males were observed hunting mainly close to the nesting site, usually within a radius of two or three kilometres, although occasionally much larger distances were recorded. *C.c.* females usually did not hunt farther than ca 1 km. from the nest. In only one case, in Flevoland, one *C.c.* female was regularly observed as far as ca. 5 km. from the nest, but this represented a case of an isolated nest of *C.c.* in an area where harriers, especially *C.a.*, bred scattered over the area and seldom close together (Schipper, 1973). *C.a.* females hunted more frequently near their nests than did males in Flevoland, thereby often encountering *C.c.* females, but, on the average, *C.a.* females flew farther from the nest than did *C.c.* females.

In all of the study areas *C.c.* males were observed to hunt most frequently at distances of three or more kilometres from the nest; *C.p.* males probably even exceeded distances of twelve km. In Ameland, Terschelling, Groote Peel, Northern and Southern France *C.p.* females almost always stayed within a radius of about 1 km., but in Flevoland, one of them has been observed hunting to as far as about 6 km. from the nest, in this way showing the same tendency as the males.

It will be evident that particularly where several species of harrier nest in close proximity, the differences in hunting behaviour described above contribute to the possibility of different harrier species and sexes hunting in different areas. At the same time these differences induce new inter- and intraspecific differences in food composition, as the hunting areas visited may yield local differences in prey supply.

Interspecific differences in prey weight were greater in females than in males (Figure 12), the small sexual dimorphism in foot size (NIEBOER, 1973) and body size in *C.p.* contributing to this general picture. The smaller interspecific differences in the males may be related to the noteworthy differences in their hunting distances, whereas the females with their larger interspecific differences in average prey weight generally hunt in the vicinity of their nests (See also Figure 9 and discussion in Chapter 9.1.2.).

A further correlation may exist between prey weight in relation to body weight and hunting distances : *C.p.* males hunting over large distances and taking relatively small prey, *C.a.* females and *C.c.* females staying close to their nests and taking large prey, *C.a.* males dispersing further than their females, and *C.c.* males further than *C.a.* males, the first named categories taking on the average larger prey than the second ones. Although the low average prey weight in *C.p.* females is not clear, hunters over longer distances from the nests tended to supply the smalles prey items to their young, hunters over shorter distances the largest ones. This may be related to the difficulties involved, when carrying a large prey to the nest (See Chapter 6.2.1.)

9.2.6. Agility of prey.

Though it seems that most of the harrier food does not require a great agility on the part of the hunting bird, some prey animals particularly full-grown songbirds are rather agile and can be caught only by surprise or after a dexterous pursuit. Taking full-grown Passeriforme birds as a measure of great hunting dexterity and considering carrion and bird eggs as most easily obtainable Table 34 may give an impression of interspecific differences in agility.

Table 34: Comparison of agile and easily obtainable prey in harrier food, according to nest observations.

Prey category	Percentage in food/occurrence		
	C.p.	*C.c.*	*C.a.*
Passeriformes (no pulli included) .	35	48	7
Carrion (regularly observed) . .	—	—	+
Bird eggs (regularly observed) . .	+	—	+

C.c. proved to take more agile prey items than the other harrier species, *C.a.* took the smallest relative numbers. In contrast *C.a.* took more carrion and eggs, which were not observed in the food of *C.c.* (carrion and eggs are occasionally eaten by *C.c.*, see Dement'ev *et al.* (1951). In addition, *C.c.* has been observed to hunt more frequently with a speed and manoeuvrability, adjusted to surprise agile prey, than *C.p.* and *C.a.* (SCHIPPER, *et al.*, in prep.).

In all harrier species studied, males hunted over larger distances than did the females and thus would have a better chance of meeting with motionless prey (bird eggs and carrion). Indeed, only males regularly were observed to take bird eggs and carrion (*C.a.*) or bird eggs (*C.p.*).

With the exception of Flevoland, 1972, the highest percentages of Passeriforme birds (no pulli included) were always taken by *C.c.* males, followed by *C.p.* males (Ameland and Terschelling) and *C.c.* females (Flevoland), see Table 35. In Flevoland, 1971, *C.p.* males supplied less agile prey than did females, in contrast to the observations in all other study areas. Obviously *C.p.* males and females, as well as *C.c.* females, also possess sufficient dexterity to prey to a considerable extent upon full-grown songbirds. In *C.a.* predation on this prey category has been observed only in males.

Table 35: Passeriformes (no pulli included) in food, observed during nest observations.

Species and sex	Ameland	Terschelling		Flevoland		S. France	Total
	1967/70	1962	1968	1971	1972	1969	
C.p. ♂	36	25	49	25	—	44	36
C.p. ♀	15	17	48	29	—	7	23
C.c. ♂	42	69	53	48	18	—	48
C.c. ♀	19	12	37	40	22	—	26
C.a. ♂	—	—	—	15	—	0	8
C.a. ♀	—	—	—	0	—	0	0

Our observations concerning agility indicate that *C.c.* is the most agile species, a conclusion which does not concur with NIEBOER (1973), who considered *C.p.* to be the most agile.

Observations during winter showed that in the food of *C.a.* easily obtainable prey such as disabled or dead animals predominated. *C.c.* preferred voles, where these were numerous, but appeared to be able to prey upon Passeriforme and other birds to a great extent, whereas the taking of carrion was never observed. Although the food taken during the breeding season and in winter was not the same, the conclusions concerning agility of the prey taken by *C.a.* and *C.c.* in the breeding season were confirmed by the winter observations.

9.2.7. *Habitat selection.*

One may assume that each of the harriers generally search for prey most frequently in those habitats where vegetation and landscape, apart from the presence of potential prey, enable them to hunt with success. Assuming also that the structural characteristics of the species are adjusted to the requirements of hunting in particular habitats, interspecific and intraspecific differences in habitat preference may induce differences in prey selection.

One may assume further that within the hunting territory each individual is well acquainted with those sites where particular prey species are numerous and can be easily captured. Provided this assumption is true it must be considered to define the ultimate habitat selection, as the harrier prefers hunting in these particular places.

In search for a particular prey the harrier may adjust its speed, altitude and other flying properties to the expected prey species. These adjustments may be considered to be adaptations to a «searching image», as proposed by Tinbergen (1960). Other prey species, if met with, may therefore have a greater chance to escape, but incidentally may be captured as well and thereby become an additionally searched for source of food in the same habitat. An example of this will be given.

In Flevoland, winter 1970, C.c. obviously preferred to prey upon voles in extensive agricultural fields (Table 16). Birds and *Micromys minutus*, most of them occupying marshy areas, comprised not more than 7% and 5% of the food, respectively. In winter 1971, when voles were much scarcer, C.c. had turned to prey upon birds in the marshy areas to a considerable extent (50%). Simultaneously the amount of the less important prey species *Micromys minutus* had risen from 5% to 14%.

Therefore, even if two species or sexes of harrier display distinctly aimed prey preferences (searching images) in different or the same habitats, the mechanism of adjustability described above helps to assimilate the differences and gives rise to inter- or intraspecific overlaps in food composition. The extent of this type of overlap in inter- and intraspecific interrelationships, is however beyond our means to measure.

10. GENERAL DISCUSSION AND CONCLUSIONS.

Although many authors have published data on the food of harriers, a reliable comparison with our nest observation data is not always possible, since results of analysis of pellets and prey remnants, or a combination of several food analysis methods (analysis of pellets, prey remnants, stomach contents, nest observations and casual field observations) are often involved.

Food studies of C *a.* in Ameland and Terschelling (ROOTH, 1956 and 1963) revealed rabbits to be an important prey category, which agrees with the conclusions of our study. In the Peel, as in Groote Peel in the present study, many young *Larus ridibundus* were taken (Haverschmidt, 1940). An unpublished study by Weber (1966) in Camargue mentions young nidifugous water birds and snakes, observed in the food of C.*a.* during nest observations; rabbits were observed less frequently than in our study. HOSKING (1943) observed a rather large amount of larger mammals, among which rabbits and leverets, supplied to the young during nest observations in Norfolk, England. Young nidifugous birds were frequently recorded in many areas : Finland (HILDEN and KALINAINEN, 1966), Germany, Hungary and France (UTTENDÖRFER, 1939 and 1952), Lake Neuchatel, Swiss (Blanc and Manuel, 1956), Belgium (Verbruggen, 1968), Spain (Valverde, 1960) and U.S.S.R. (DEMENT'EV, 1951), the observed prey often including water birds. BAKKER (1955) and KORIDON (according to D. JONKERS, pers. comm.) recorded noteworthy predation on frogs, TEN KATE (1930) on fish and frogs in Holland in Noordoostpolder, Zwarte Meer and Kampereiland, respectively.

In contrast with the present study, several authors frequently observed small mammals like voles in the food of C.*a.* : Bakker (1955) in Noordoostpolder, Holland, THIOLLAY (1967) in Lorraines, France, HILDEN and KALINAINEN (1966) in Finland, Uttendörfer (1939 and 1952) in Germany, Hungary and France, and Pinowski (1961) in Poland. In Noordoostpolder voles were extremely abundant and heavy plagues occurred (BAKKER, 1955 and 1957; BAKKER and VAN DER ZWEEP, 1950). During our studies in breeding time, such plagues were not observed, and heavy predation by C.*a.* on voles probably is restricted to situations where these animals are very numerous. As voles are not very agile, it is not surprising that during a period of sufficient supply C.*a.* preys upon them, and the short span of time, required for the localizing of a new prey item, may compensate for its small size.

Bird eggs were recorded as food of C.*a.* in Germany and Hungary (UTTENDÖRFER, 1939 and 1952; MARTENS, 1964), in Kampereiland, Holland (TEN KATE, 1930), in France (THIOLLAY, 1967), in Spain (VALVERDE, 1960) and in U.S.S.R. (DEMENT'EV, 1951).

Predation by C.*a.* on aquatic and marsh animals and larger mammals, like rabbits, as recorded by many authors, concurs with the results of the present study.

Concerning C.*c.* the literature reveals data which corresponds well with those of the present study. Passeriforme birds and particularly small mammals like voles were observed to be frequently taken in many areas : Fennoscandia (BERGMAN, 1961), Germany, Hungary and France (UTTENDÖRFER, 1939 and 1952), Drauszensee, Germany

(HAAS, 1939), Lüneburgerheide, Germany (nest observations by HENNINGS, 1936), Orkney, Scotland (nest observations by BALFOUR and MACDONALD, 1970), and U.S.S.R. (DEMENT'EV, 1966). In addition voles were much taken by *C.c.* in Ameland (ROOTH, 1963), and songbirds in Terschelling (ROOTH, 1956).

Generally voles were recorded more frequently in those studies than in the present one, which, as in *C.a.* may be due to greater abundance of this prey species in the areas involved.

Rabbits were an important prey category in Ameland and Terschelling (ROOTH, 1956 and 1963). Additionally, nidifugous land birds were taken in some areas to a greater or lesser extent : Fennoscandia (BERGMAN, 1961), and Drauszensee, Germany (HAAS, 1939). Lizards and insects were occasionally recorded (UTTENDÖRFER, 1939), whereas DEMENT'EV (1951) also reports these prey categories of *C.c.* in U.S.S.R. Fish, frogs and snakes in the diet have been recorded in Great Britain (GLUTZ VON BLOTZHEIM *et al.*, 1971), bird eggs in Germany (UTTENDÖRFER, 1939), in Hungary (BITTERA, 1914) and the U.S.S.R. (DEMENT'EV, 1951).

In *C.p.*, ROOTH (1963) observed many voles in the food in Ameland, lizards (ROOTH, 1956) in Terschelling. LIEFTINCK (1922) observed mainly songbirds among the food in Drente, Holland. Small mammals like voles, and Passeriforme birds were frequently observed as prey of *C.p.* in Vendée, France (THIOLLAY, 1968; only a few songbirds), in Germany, Hungary, U.S.S.R. and France (UTTENDÖRFER, 1939 and 1952), and in U.S.S.R. (KHUSIANOV, 1963; DEMENT'EV, 1951). Insects were frequently observed in Vendée, France (THIOLLAY, 1968), in U.S.S.R. (DEMENT'EV, 1951), in Germany, Hungary and France (UTTENDÖRFER, 1939 and 1952), bird eggs in Germany, Hungary and France (UTTENDÖRFER. 1939; MARTENS, 1964), in Vendée, France (THIOLLAY, 1968) and in U.S.S.R. (DEMENT'EV, 1951).

Although in all three harrier species, during former food studies voles were taken more frequently than observed in the present study, the general picture is the same, and the interspecific differences in prey selection, discussed before, are not denied.

From the present study the three harrier species involved proved to be characterized by inter- and intraspecific differences in food composition, which probably were achieved by predation differences in time and space, and by predation differences directly related to intrinsic, morphological and structural properties. Interspecific differences in breeding time and consequently different periods of maximum predation, which also intraspecifically were different, achieved an inter- and intraspecific partition in time, and consequently in prey selection. Furthermore the harriers showed inter- and intraspecific differences in habitat selection and distances, across which they withdrew from the nest when hunting. Inter- and intraspecific differences in skilfulness probably achieved differences in prey composition as to the amount of agile prey taken, whereas different harrier species and sexes took prey of more or less different size. Possibly certain types of weather were of different influence on each of the harrier species; the activity of prey animals would also be effected, thus achieving further interspecific differences in food composition.

For a good understanding of the different roles of males and females in the supply of food to the young, varying in the course of the nestling period and during the day, and discussed in Chapter 9.1.2. and 9.2.3., the observation periods at the nest should cover a longer spell of time than was usually the case in our studies, whereas the observations at nests of different harrier species should be more synchronic in order to obtain more perfect possibilities of comparison.

Still some noteworthy results have to be discussed. In Chapter 9.2.6. *C.c.* has been considered to be the most agile of the three species, which does not concur with the conclusion of NIEBOER (1973), who called *C.p.* the most agile, as *C.p.* has a longer tail in relation to the average body weight, and is supposed to fly lower when hunting. The latter feature has not been confirmed by field studies. However, when not measured in relation to body size but in relation to wing length, *C.c.* appears to have the longest tail (according to measurements, presented by the same author). Elsewhere NIEBOER considered the larger tail/wing ratio in *C.c.* to be a possible consequence of specialization on smaller and probably more agile prey requiring increased manoeuvrability, which opinion very well fits in the results of the present study. In addition a long tail is not only related to great manoeuvrability but also to the possibility of flying slowly, e.g. when quartering the ground in search for prey (BROWN and AMADON, 1968). The more fingered wings of *C.c.* in relation to *C.p.* and the relatively short, broad wings, together with the long tail giving an *Accipiter-like* appearance to *C.c.*, may enable the bird to sprint in a pursuit of flying birds over a short distance and increase its agility.

The present study confirms that *C.a.* is the least agile of the three species (NIEBOER, 1973). As to the flying altitude when hunting, *C.c.* may fly lowest, in order to surprise agile prey, *C.a.* highest in search for slower moving prey, and making use of tall vegetation in order to achieve a surprise effect when encountering prey.

The observations concerning males taking more agile prey than females fit very well with the opinion of NIEBOER (1973), that the predominantly grey and countershaded adult male plumages in harriers are advantageous while hunting prey with keen vision in open terrain.

The locally high frequency of lizards and insects in the food of *C.p.* may be explaned by the relatively short toes and claws of this species (for measurements see NIEBOER, 1973), and partly to its hunting habits, whereas the observed intraspecific difference in *C.a.* as to preying upon snakes by males only, may be due to the same feature, the male having shorter toes and claws than the female. Of particular interest was the supply of living prey specimens by a *C.a.* male and a *C.p.* female, which may be due to the large feet of the harriers in relation to the small prey.

In relation to their ranges in Spain and Italy (Voous, 1960), the observed differences in prey selection in *C.c.* and *C.p.* are of particular interest, as in large areas of these countries *C.c.* does not breed where *C.p.* (and also *C.a.*) occurs. The present study found that in Terschelling the lack of voles did not induce *C.c.* to take lizards as did *C.p.* It may be possible, therefore, that the absence of *C.c.* in the above mentioned areas is related to the lack of *Microtus arvalis* (Van den Brink, 1968) and replacements accessible to *C.c.* Note also the food of *C.c.* in Italy in winter (Chapter 7.2.). Although *C.c.* appeared to be able to prey on other prey categories, voles still seem to be an important food item.

During the breeding season *C.p.* preyed upon young birds, lizards or insects to a great extent, whereas *C.a.* took many young animals and carrion. The migration habits of these harrier species may be related to lack or inaccessability of these prey categories in their breeding ranges in winter. Only *C.c.* may be able to support itself with agile prey (adult birds) and voles (where abundant) in the temperate and Mediterranean zones.

In Chapter 9.2.5. evidence was presented that sexual dimorphism in size and structure of harriers give rise to differential prey size selection, a feature also found in other predatory birds by Storer (1966), Hoglund (1946) and Earhart & Johnson (1970). According to Reynolds (1972) the smaller size of the male, especially in the genus *Accipiter*, may be related to its role as the more efficient forager of the pair, able to feed on very agile species. In contrast the female, starting to hunt only when the nestlings are medium sized, is able to capture from a broader prey-size range. Both conclusions were confirmed during the present study concerning harriers. Another feature related to sexual dimorphism became evident. Relying upon intrinsic and environmental factors, the largest harrier species, *C.a.*, is the first breeder, the smallest species, *C.p.* the last one. In this ecological context, and as the male always starts predation activity, the female beginning later, inter- and intraspecific partition of food-resources and hence differential niche utilization is optimally enhanced only if the males are smaller than the females (see Fig. 7 and discussion elsewhere).

Earhart & Johnson (1970) argued that the lack or reduction of sexual size dimorphism in insectivorous owls is related to the fact that they feed on a food source which consists of items of relatively small size, which exists as numerous fragments in the environment. Among harriers the small sexual size dimorphism in *C.p.*, the species most frequently preying upon small prey species, supports this proposition.

The present study has been based chiefly on prey numbers and to a lesser extent on prey biomass. Where the three harrier species are breeding close together, and select their prey from potentially the same resource of food, competition may occur if species and sex A for some reason takes prey items which are optimal and most acceptable for

Nest observations revealed that *C.p.* supplied the greatest number of prey items per unit time and per young, *C.a.* providing the smallest (Table 18). Hence a comparison of only percentages of each prey category in the food does not give reliable insight in the interspecific differences and similarities, and the number of prey items per unit time should be involved. In addition, during the nestling period males and females do not share in the prey supply to the young in a constant ratio, therefore their changing activity should also be considered to give a reliable comparison of the food compositions. Another factor to be considered is the number of prey items per unit time and per young related to the average prey weight (Fig. 4).

On the average *C.a.* nested first in the breeding season, *C.p.* being the latest breeder (Fig. 5). As the share of the females in the prey supply to the young gradually increases, the share of the males decreases (Fig. 6), the periods of maximum predation pressure exerted by males and females of the three harrier species therefore appear to be separated by periods of time. This partition in time appeared to establish that harriers of very different body weight, and hence of differing predation potential, most frequently hunt together. Harriers of less differing (i.e. similar) body weight are separated in time, and so less frequently hunt at the same time (Fig. 8). As males start their hunting activity at the beginning of the breeding season, the females starting later when the young are medium sized, the above mentioned effect is present if the males are smaller in body weight than the females. This conclusion is of importance in the discussion concerning the function and origin of sexual dimorphism among birds of prey, particularly the question of the origin of the males smaller size.

Rain caused the prey supply to the nests to decrease (Table 22), whereas in Flevoland *C.c.* and *C.p.* tended to supply birds during periods of higher wind velocity relative to quieter times when more voles were brought to the young (Table 23). On the average *C.c.* and to a lesser extent *C.p.* tended to supply more prey items to the young at high wind velocity, *C.a.* at low wind velocity (Table 24). Possibly interspecific different influences of the weather are able to influence hunting activity and prey selection, and hence the interspecific differences and similarities in prey composition.

These are also influenced by changing prey densities, which do not necessarily have the same consequences in the food composition of all three harrier species. For instance the presence of lizards in Terschelling in contrast to Ameland and Flevoland, only exhibited an influence on the food of *C.p.* In addition individual variation and specialization on particular prey species are able to influence the inter- and intraspecific relationships in prey composition.

The difference in breeding time between the three species implies that on the average, the prey densities during the nestling time is different from species to species, which is reflected in the food taken, e.g. in the course of the nestling time increasing predation on lizards by *C.p.*

The daily rhythm, measured by means of the number of prey items supplied to the nests, showed inter- and intraspecific differences. The daily activity probably depended on the activity of the prey species mainly taken, whereas only a few features in the activity pattern of the harriers should be attributed to intrinsic factors, e.g. the gradual increase and decrease in activity during the day in *C.c.* and *C.p.*, respectively, as well as start and termination of the daily activity.

On the average *C.a.* supplied heavier prey to the young than did the other harrier species, in absolute terms as well as in relation to body weight; whereas *C.p.* took the smallest prey items (Fig. 12). *C.a.* frequently brought very small prey (songbirds) to the young only in Northern France, the prey species usually taken probably being absent in the area considered.

Intraspecific average prey weight differences, as well as interspecific differences relating to the size of the foot (NIEBOER, 1973), were present in *C.a.* and *C.c.*

The interspecific differences in average prey size were greatest in females. The small interspecific differences in males may be related to the hunting habits, which are very different particularly in the males. Males of *C.p.* hunt furthest from the nest, being observed at distances exceeding 12 km, whereas the males of *C.a.* frequently hunted within a radius of 2 km from the nest. *C.c.* males were often more than 3 km from the nest. In this way the males of the three species preyed in different areas, although they bred in a common nesting area. The females, showing greater interspecific differences in mean prey weight, hunted more frequently in the surroundings of the nests, regularly frequenting the same area simultaneously.

As to the capture of agile and manoevrable prey *C.c.* probably is the most dexterous species (Table 34). C.c. took more juvenile and adult songbirds than did the other harrier species, whereas motionless prey like carrion and bird eggs were not observed, and only occasionally recorded in former studies. In contrast, C.*a.* regularly took carrion and bird eggs; songbirds able to fly were only occasionally captured. C.*p.* held an intermediate position, but it is much more dexterous than C.*a.*

In all three species males supplied more juvenile and adult songbirds to the nests as a rule than did the females, the females possibly being less dexterous. The conclusion concerning interspecific differences in agility was confirmed by the winter observations, which gave evidence that C.*a.* frequently took wounded animals and carrion, whereas C.c. preyed upon songbirds to a considerable extent, if voles were not numerous.

Although, discounting the prey densities, harriers may predominantly prey in habitats where vegetation and structure of the terrain enables them to hunt with success, e.g. habitats that enable them to surprise their prey, familiarity with the hunting range and particularly with places where the prey density is high, may define the ultimate habitat selection. In search of a particular prey species, the harrier may adjust its speed, altitude and other flying properties to the expected prey in the particular area; other prey species, if met with, may therefore have a greater chance to escape. But occasionally they may be captured as well and theoretically harriers with different prey preference may consequently show overlap in food capture, not directly relating to their prey preference. The extent of this type of overlap inter- and intraspecific interrelationships, is however beyond our means to measure.

Although inter- and intraspecific differences and similarities in food composition were present, the prey selection apparently is determined by various intrinsic, morphological and structural properties of the harriers as well as by the predation differences in time and space mentioned above, which enable the three harrier species to coexist without obvious interspecific competition for food.

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13. SAMENVATTING.

Aangezien er plaatsen zijn waar de drie Westeuropese kiekendiefsoorten, de bruine kiekendief (in het artikel afgekort als *C.a.*), de blauwe kiekendief (afgekort als *C.c.*) en de grauwe kiekendief (afgekort als *C.p.*), dicht bij elkaar broeden en er ogenschijnlijk dezelfde leef- en jachtwijze op na houden, is het van belang te weten of er interspecifieke competitie optreedt, of dat de soorten dusdanig in hun oecologie verschillen, dat ze zonder competitie naast elkaar kunnen leven. Het artikel gaat daartoe in op verschillen in voedselkeuze, terwijl publicaties betreffende jachtgedrag en broedbiologie nog zullen verschijnen.

Door middel van schuilhutwaarnemingen bij nesten, aangevuld met o.a. braakbalanalyses en analyses van prooiresten, werd de voedselsamenstelling van de drie soorten kiekendieven vastgesteld gedurende een aantal jaren in het broedseizoen (Tabel 2), terwijl het voedsel van *C.a.* en *C.c.* in de winter werd bestudeerd aan de hand van braakballen (Tabel 3). Een discussie over de voor en nadelen van deze verschillende methodes van voedselanalyse is te vinden in hoofdstuk 5. Schuilhutwaarnemingen bleken de grootste betrouwbaarheid op te leveren. Zie voor het vastgestelde voedsel gedurende de schuilhutwaarnemingen Tabel 6, voor aanvullende waarnemingen Tabel 7, 8 en 9. Het voedsel in de winter is weergegeven in Tabel 15 en 16.

De grootste interspecifieke overlap in voedselsamenstelling werd gevonden in vier prooicategorieën, te weten jonge steltlopers en fazanten (8), zangvogels (9), zoogdieren van muisgrootte (10) en grotere zoogdieren (11), zie Tabel 6. Deze overlap bleek bij nadere uitwerking het grootst te zijn bij de predatie op jonge fazanten, op vliegvlugge zangvogels (zonder spreeuwen), op veldmuizen en op jonge konijnen (zie Tabel 13). Verder vertoonden mannetjes en wijfjes een verschillende voedselkeuze. Deze wordt voor drie gebieden vergeleken in Fig. 2.

In de winter bleek *C.c.* vooral te jagen op twee categorieën voedsel, te weten veldmuizen en zangvogels, waarbij in gebieden met veel veldmuizen deze prooisoort werd geprefereerd. *C.a.* maakte veel jacht op watervogels, vermoedelijk vooral als deze verziekt, gewond of dood waren. Van *C.p.* is weinig over het voedsel in de winter bekend.

Een vergelijking van het voedsel in de broedtijd met de geschatte prooidichtheden in de onderzoeksgebieden (Tabel 4) maakte duidelijk dat *C.a.* voornamelijk water- en moerasdieren (vissen, kikkers, ringslangen, ralachtigen, maar in Flevoland ook fazanten) en konijnen uit de duinen at, die dus overwegend in de betreffende biotopen moeten zijn gevangen. In het voedsel van *C.c.* kwamen ook wel prooien uit deze biotopen voor, zoals rietvogels en konijnen, maar in verhouding tot *C.a.* werden veel meer open land vogels, zoals leeuweriken, gevangen. Deze tendens was bij *C.p.* nog sterker. Gesteld kan worden dat, hoewel alle kiekendiefsoorten jagen boven zowel de broedgebieden met vaak dichte en hogere opgaande begroeiing (duinen en moeras) als boven de omliggende landbouwgebieden en weiden, bij *C.a.* de nadruk ligt op de eerstgenoemde biotopen, bij *C.p.* op de laatstgenoemde, terwijl C.c. in dit opzicht een middenpositie inneemt (Fig. 3). Bij alle drie de soorten joegen de wijfjes meer in de omgeving van het nest, en dus boven meer gestructureerde vegetatie, dan de mannetjes.

Uit de schuilhutwaarnemingen bleek dat per jong *C.p.* het grootste aantal prooien per tijdseenheid aanvoerde, *C.a.* het kleinste aantal (Tabel 18). Dientengevolge geeft een vergelijking van alleen de percentages van elke prooicategorie in het voedsel geen zuiver beeld van de interspecifieke verschillen en overeenkomsten, en moeten deze percentages worden ingepast in het aantal prooien per tijdseenheid. Bovendien is de verhouding tussen het aantal prooien, aangevoerd door mannetjes en wijfjes, gedurende de jongentijd niet constant, zodat ook hun wisselend aandeel in de prooiaanvoer ten behoeve van een relevante vergelijking zou ingepast moeten worden. Voorts bleek een verband aanwezig tussen het aantal prooien, per jong per tijdseenheid aangevoerd, en het gemiddelde prooigewicht (Fig. 4).

Gemiddeld broedde *C.a.* het vroegst in het jaar, *C.p.* het laatst (Fig. 5). Gezien dit feit, en daar het aandeel van de wijfjes in de prooiaanvoer voor de jongen geleidelijk toeneemt, terwijl het aandeel van de mannetjes afneemt (Fig. 6), bleek er gemiddeld een verdeling in tijd te bestaan, waarin de mannetjes en wijfjes van de drie kiekendiefsoorten hun maximale predatiedruk uitoefenden. Deze verdeling bleek zodanig te zijn, dat vooral kiekendieven van sterk verschillend lichaamsgewicht, en dus verschillend

predatiepotentieel, het meest tegelijk jagen, terwijl kiekendieven met kleinere verschillen in lichaamsgewicht in dit opzicht in de tijd zijn verdeeld en dus minder tegelijk jagen (Fig. 8). Aangezien altijd de mannetjes eerst jagen, terwijl de wijfjes pas later actief worden wordt dit effect vooral bereikt als de mannetjes kleiner zijn dan de wijfjes, een constatering die van belang is in de discussie rond de vraag naar het waarom van de sexuele dimorfie in grootte bij roofvogels, en inzonderheid de vraag waarom juist de mannetjes kleiner zijn.

Regen bleek een remmende invloed op de prooiaanvoer bij het nest te hebben (Tabel 22), terwijl in Flevoland *C.c.* en *C.p.* er toe neigden vogels gemiddeld tijdens perioden met hogere windsnelheid aan te voeren dan muizen (Tabel 23). De tendens was aanwezig dat bij *C.c.*, en in mindere mate bij *C.p.*, een hogere windsnelheid samen viel met een versterkte prooiaanvoer, bij *C.a.* met een geringere prooiaanvoer (Tabel 24). Interspecifiek verschillende invloeden van het weer kunnen dus mogelijk de jachtactiviteit en prooikeuze, en derhalve de interspecifieke verschillen en overeenkomsten in prooisamenstelling beïnvloeden.

Deze kunnen ook worden beïnvloed door veranderingen in het prooiaanbod, die niet in de voedselsamenstelling van alle drie de kiekendiefsoorten dezelfde gevolgen hoeven te hebben. Zo is het voorkomen van hagedissen op Terschelling, in afwijking van Ameland en Flevoland, alleen sterk terug te vinden in het voedsel van *C.p.* Ook individuele variatie en specialisatie op bepaalde prooidiersoorten kan de inter- en intraspecifieke verhouding in prooisamenstelling beïnvloeden.

Het verschil in broedtijd tussen de drie soorten brengt met zich mee dat gemiddeld in de jongentijd van de ene soort het prooiaanbod verschilt van dat in de jongentijd van de andere soort, hetgeen in het voedsel is terug te vinden. Dezelfde factor speelt een rol in de tijdens de jongentijd toenemende predatie van *C.p.* op hagedissen of insecten.

Het dagritme, gemeten naar het aantal prooien dat bij de nesten werd aangevoerd, vertoonde inter- en intraspecifieke verschillen. Vermoedelijk was het dagrithme, sterk afhankelijk van de activiteit van de belangrijkste prooien, terwijl slechts enkele verschijnselen in het activiteitspatroon van de kiekendieven vermoedelijk moeten worden toegeschreven aan inwendige factoren, zoals respectievelijk de geleidelijke activiteitsafname en toename over de dag bij *C.p.* en *C.c.*, alsmede het begin en eind van de dagactiviteit.

Gemiddeld bracht *C.a.*, ook in verhouding tot het lichaamsgewicht, zwaardere prooien aan de jongen dan de andere soorten, terwijl *C.p.* de lichtste prooien aanbracht (Fig. 12). Alleen in Noord-Frankrijk werden bij een nest van *C.a.* veel zeer kleine prooien aangevoerd (zangvogels), hetgeen vermoedelijk samenhing met het ontbreken van de normale prooidieren in het betreffende gebied.

C.a. en *C.c.* vertoonden intraspecifieke verschillen in gemiddeld prooigewicht, welke evenals de interspecifieke verschillen samenhangen met de grootte van het vangapparaat (NIEBOER, 1973).

De interspecifieke verschillen in gemiddelde prooigrootte waren het grootst tussen de wijfjes onderling. Dat deze verschillen tussen de mannetjes onderling kleiner zijn zou verband kunnen houden met het feit dat vooral de mannetjes sterk verschillen in jachtgewoonten. De mannetjes van *C.p.* jagen het verst weg van het nest, en werden op meer dan 12 km daarvandaan waargenomen, terwijl de mannetjes van *C.a.* dikwijls binnen een straal van 2 km tot het nest joegen. *C.c.* mannetjes verwijderden zich dikwijls 3 of meer km van het nest. Op deze wijze joegen de mannetjes van de drie soorten, komend uit een gemeenschappelijk broedgebied, in verschillende gebieden. De wijfjes, met hun grotere interspecifieke verschillen in gemiddeld prooigewicht, joegen veel meer in de omgeving van het nest, waarbij ze regelmatig tegelijk in hetzelfde gebied kwamen.

Vermoedelijk is *C.c.* de meest wendbare soort van de drie, waar het gaat om het grijpen van snelle en lenige prooien (Tabel 34). *C.c.* nam de meeste juveniele en adulte zangvogels, terwijl onbeweeglijke prooien als aas en eieren van vogels nimmer werden geconstateerd, en ook in de literatuur weinig vermeld worden. *C.a.* daarentegen at regelmatig aas en eieren, terwijl vliegvaardige zangvogels slechts weinig werden gegrepen. *C.p.* nam wat dit betreft een tussenpositie in, maar is veel wendbaarder dan *C.a.* Bij alle drie de soorten voerden de mannetjes als regel meer vliegvaardige zangvogels aan bij het nest dan de wijfjes, zodat de laatsten mogelijk als minder wendbaar beschouwd moeten worden. De winterwaarnemingen, waaruit bleek dat *C.a.* veel gewonde dieren en aas at, terwijl *C.c.* bleek in aanzienlijke mate van zangvogels te kunnen leven, bevestigden de bovenstaande conclusie betreffende de interspecifieke verschillen in wendbaarheid bij deze soorten.

Hoewel, afgezien van het prooiaanbod, de kiekendieven vooral prooien zullen zoeken in biotopen, met een vegetatie en structuur die hen in staat stelt met succes te jagen, men denke bijv. aan verrassingseffect, zal uiteindelijk bekendheid met het jachtgebied en in het bizonder met plaatsen waar de prooidichtheid groot is, bepalend zijn voor de biotoopkeuze. Als de jagende vogel zijn vliegsnelheid, vlieghoogte en andere eigenschappen van het vliegen, afstelt op de verwachte prooisoort in een bepaald gebied, zullen andere prooisoorten, ook al worden deze opgemerkt, minder kans hebben om gegrepen te worden. Toch kan dit voorkomen, en theoretisch kunnen kiekendieven met verschillende prooivoorkeur, ten gevolge van het beschreven verschijnsel, overlap in voedselsamenstelling vertonen, die niet direct met hun prooivoorkeur samenhangt. In feite ontsnappen de consequenties van dit verschijnsel in een onderzoek als dit echter grotendeels aan de waarneming.

Hoewel behalve inter- en intraspecifieke verschillen in prooisamenstelling ook overeenkomsten aanwezig waren, bleek de prooikeuze het gevolg van verschillende inwendige, morphologische en structurele eigenschappen, zowel als van de bovengenoemde predatieverschillen in tijd en ruimte, die de kiekendiefsoorten in staat stellen zonder duidelijke interspecifieke voedselconcurrentie in een gebied sympatrisch voor te komen.

14. RESUME.

Les trois busards d'Europe occidentale, le Busard des roseaux, *Circus aeruginosus* (*C.a.*), le Busard Saint-Martin, *Circus cyaneus* (*C.c.*) et le Busard cendré, *Circus pygargus* (*C.p.*) nichant côte-à-côte dans diverses régions, semblent montrer des modes de vie et de chasse similaires. Il est donc important de savoir s'il y a compétition interspécifique, ou si, au contraire, en raison de divergences écologiques les trois espèces peuvent coexister sans compétition. Le présent article aborde ce problème par le biais de la sélection de nourriture. D'autres publications couvrant le mode de chasse et la biologie de reproduction sont en préparation.

Des observations au nid, depuis une cache, auxquelles se sont ajoutés des examens de pelotes et de restes de proie, ont permis d'établir, au cours de plusieurs saisons de nidification, le régime alimentaire des trois espèces (Tableau 2). La nourriture hivernale de *C.a.* et *C.c.* a été étudiée par l'examen de pelotes (Tableau 3). Une discussion des diverses méthodes d'étude du régime alimentaire est présentée au Chapître 5. Ce sont les observations au nid qui se sont avérées donner les résultats les plus valables. Le Tableau 6 reprend les données sur le régime, obtenues par observation au nid, les Tableaux 7, 8 et 9 les observations additionnelles. Le régime d'hiver est repris dans les Tableaux 15 et 17.

Une coïncidence de régime des diverses espèces se trouve surtout dans quatre catégories de proies : les jeunes limicoles et faisans (8), les passereaux (9), les mammifères de la taille du campagnol (10) et les mammifères de plus grande taille (Tableau 6). Un examen plus approfondi montre que ce recouvrement est le plus grand dans la prédation des jeunes faisans, des passereaux jeunes et adultes (étourneaux non compris), des campagnols des champs (*Microtus arvalis*) et des jeunes lapins (Tableau 13). Mâle et femelle montrent des choix de proies différents. Une comparaison interspécifique et intraspécifique des éventails de proies dans les trois secteurs d'étude est présentée dans la Fig. 2.

L'hiver *C.c.* utilise surtout deux catégories de proie, les campagnols et les passereaux, les campagnols étant préférés là où ils sont nombreux. *C.a.* attaque souvent les oiseaux d'eau, surtout les individus affaiblis, malades ou morts. On ne sait que très peu du régime hivernal de *C.p.*

Une comparaison de la fréquence de proies dans la nourriture consommée pendant la nidification avec leur abondance locale (Tableau 4) montre que *C.a.* s'empare surtout d'animaux aquatiques et de marais (poissons, grenouilles, couleuvres, râles, mais

à Flevoland, aussi faisans) et de lapins provenant des dunes, proies qui sont spécifiques à ces habitats. Dans la nourriture de *C.c.* des proies provenant de ces habitats — tels oiseaux de roseaux et lapins — sont aussi présentes, mais un nombre beaucoup plus grand d'oiseaux de terrains ouverts, comme des alouettes, sont capturés. Cette tendance est encore plus accentuée chez *C.p.* On peut dire que, bien que les trois espèces chassent dans leur habitat de nidification souvent caractérisé par une végétation dense et assez haute (dunes et marais), ainsi que dans les champs et prairies des environs, *C.a.* chasse surtout dans l'habitat de nidification et *C.p.* dans les habitats ouverts, tandis que *C.c.* est intermédiaire (Fig. 3). Chez les trois espèces les femelles chassent plus souvent dans les environs du nid et donc au-dessus d'une végétation plus forte que les mâles.

Les observations au nid montrent que *C.p.* apporte le plus grand nombre de proies par unité de temps à ses jeunes, *C.a.* le plus petit (Tableau 18). Dès lors une simple comparaison des pourcentages de chaque type de proie dans la nourriture ne donne pas une image convenable des différences interspécifiques, et le nombre de proies par unité de temps doit être introduit. De plus, pendant la période d'élevage des jeunes, le mâle et la femelle ne se partagent pas l'approvisionnement des jeunes suivant un rapport constant, de sorte qu'il faut aussi tenir compte de leur activité variable pour obtenir une comparaison valable. Un autre facteur à considérer est le nombre de proies par unité de temps et par jeune en fonction du poids moyen des proies (Fig. 4).

En moyenne, *C.a.* niche le premier, *C.p.* le dernier (Fig. 5). Comme la part prise par la femelle au nourrissage augmente progressivement (Fig. 6), les périodes de prédation maximum exercée par le mâle et par la femelle de chacune des trois espèces sont séparées par un intervalle de temps. Cette répartition des périodes de prédation semble se faire de telle façon que les busards présentant de grandes différences de poids, et donc des potentiels de prédation très différents, chassent simultanément. Les busards les plus similaires en poids chassent rarement en même temps (Fig. 8). Comme les mâles commencent leur activité de chasse au début de la saison de nidification et les femelles seulement quand les jeunes ont atteint le milieu de leur croissance, cet effet est obtenu si les mâles sont plus petits que les femelles. Cette conclusion est importante pour la solution du problème du dimorphisme sexuel chez les rapaces.

La pluie entraîne une réduction de l'approvisionnement au nid (Tableau 22). Des vitesses de vent élevées, à Flevoland, semblent correspondre pour *C.c.* et *C.p.* à un plus grand apport d'oiseaux, tandis que les campagnols sont apportés en plus grand nombre par vent calme (Tableau 23). En moyenne, *C.c.* et dans une moindre mesure *C.p.* tendent à apporter plus de proies aux jeunes par vent vif, *C.a.* par temps calme (Tableau 24). Il est possible que le temps influence les activités de chasse et la sélection des proies de façon différente pour chacune des espèces, contribuant ainsi aux divergences de régime.

Le régime est également influencé par les variations d'abondance des proies et de façon différente suivant l'espèce de busard. Ainsi la présence de lézards à Terschelling, par opposition à Alemand et Flevoland, n'a d'effet que sur le régime de *C.p.* De plus, la variation individuelle et une spécialisation pour certaines espèces de proie influencent les relations interspécifiques et intraspécifiques de régime.

Le décalage des saisons de nidification des trois espèces entraîne une différence d'abondance de proies qui se reflète dans la nourriture. Ainsi, au cours de la saison, la prédation sur les lézards augmente chez *C.p.*

Le rythme quotidien, mesuré par l'apport de proies au nid, varie d'espèce à espèce et aussi à l'intérieur d'une espèce. L'activité quotidienne dépend probablement surtout de l'activité des proies principales, et seuls certains aspects de cette activité peuvent être attribués à des facteurs intrinsèques.

En moyenne, *C.a.* apporte des proies plus lourdes que celles des deux autres espèces, aussi bien en termes absolus qu'en termes relatifs. Au contraire *C.p.* apporte les proies les plus légères (Fig. 12). Ce n'est que dans le Nord de la France que *C.a.* amène fréquemment des proies très petites (passereaux), peut-être par manque des proies habituelles. Les plus grandes différences interspécifiques dans la taille des proies s'observent chez les femelles. Ce phénomène est probablement lié aux habitudes de chasse. Les mâles des diverses espèces, même s'ils nichent en un même endroit, chassent sur des terrains différents. *C.p.* chasse loin du nid, ayant été observé à des distances supérieures à 12 km; *C.c.* a été observé à plus de 3 km; *C.a.* chasse souvent dans un rayon de moins de 2 km autour du nid. Les femelles au contraire chassent toutes souvent dans les environs du nid et donc fréquentent simultanément la même zone.

C.c. est probablement l'espèce la plus adroite (Tableau 34), prenant plus de passereaux que les autres et rarement des proies immobiles, *C.a.* la moins adroite, prenant souvent des charognes et des œufs, *C.p.* intermédiaire. Chez les trois espèces, le mâle amène plus de passereaux que la femelle. Ces différences d'agilité sont confirmées en hiver, *C.a.* prenant souvent des oiseaux blessés et des charognes, *C.c.* des passereaux, si les campagnols ne sont pas nombreux.

Si les busards chassent surtout dans des habitats ou la végétation et la configuration du terrain leur permettent d'opérer avec succès, c'est-à-dire de surprendre leur proie, c'est probablement leur familiarité avec le terrain de chasse et particulièrement avec des lieux de haute densité des proies, qui décide en dernier ressort du choix de l'habitat. A la recherche d'une certain type de proie, le busard ajuste sans doute sa vitesse, son altitude et les autres caractéristiques de son vol à la proie envisagée et au terrain concerné; dès lors, d'autres proies rencontrées peuvent avoir des chances accrues de salut. Elles seront quand même capturées occasionnellement, de sorte que des busards, dont les préférences diffèrent, montreront tout de même un certain recouvrement dans les captures, recouvrement qui n'est pas lié à leurs préférences. Il nous est impossible d'évaluer ce recouvrement accidentel.

La sélection des proies semble donc déterminée et par des caractères morphologiques intrinsèques des busards et par des différences spatiales et temporelles de prédation, ce qui permet aux trois espèces de coexister sans compétition évidente pour la nourriture.

APPENDICES

Appendix 1: Prey numbers observed in *Circus aeruginosus*.

	Nest observations									
	Ameland	Terschelling	Flevoland			N. France		S. France		
	1964	1959	1971			1970		1969		
	+ 1♀	1♂ + 1♀	2♂♂	2♀♀	Σ	1♀	1♂ + 1♀	3♂♂	2♀♀	Σ
Large insect	—	—	—	—	—	—	—	—	—	—
Hydrous piceus	—	—	—	—	—		—	—	—	—
Fish	—	—	—	—	—	—	—	2	—	2
Eel	—	—	—	—	—	—	—	2	2	4
Frog	—	—	—	—	—	—	—	12	1	13
Snake	—	—	—	—	—	—	—	22	—	28
Lizard	—	—	—	—	—	—	—	—	—	—
Anas species pullus	—	—	—	—	—	—	—	—	—	—
Anas species juvenile/adult	2	—	2	1	4	—	—	—	—	—
Anas platyrhynchos adult	—	—	—	—	—	—	—	—	—	—
Anas crecca/querquedula	—	—	—	—	—	—	—	—	—	—
Somateria mollissima pullus	—	2	—	—	—	—	—	—	—	—
Rallidae pullus	—	—	—	—	—	—	—	2	—	3
Rallidae juvenile/adult	—		—	—	—	—	—	—	—	—
Rallus aquaticus pullus	—	—	—	—	—	1	1	—	—	—
Rallus aquaticus juvenile	—	—	—	—	—	—	—	—	—	—
Rallus aquaticus juvenile/adult	—	—	—	—	—	—	—	—	—	—
Rallus aquaticus adult	—	—	—	—	—	—	—	—	—	—
Porzana porzana	—	—	—	—	—	—	—	—	—	—
Porzana pusilla	—	—	—	—	—	—	—	—	—	—
Crex crex	—	—	—	—	—	—	—	—	—	—
Gallinula chloropus pullus	—	—	—	—	—	1	1	—	—	2
Gallinula chloropus juvenile	—	—	—	—	—	1	1	1	—	1
Gallinula chloropus adult	—	—	—	—	—	—	—	—	—	—
Fulica atra pullus	—	—	—	—	—	—	—	1	5	16
Fulica atra juvenile	—	—	—	—	—	—	—	3	1	7
Perdix spec. pullus	—	—	—	—	—	—	—	2	—	2
Coturnix coturnix	—	—	—	—	—	—	—	—	—	—
Phasianus colchicus pull./juv.	2	—	10	7	39	—	—	—	—	—
Limicolae	—	—	—	—	—	—	—	—	—	—
Haematopus ostralegus pullus	—	1	—	—	—	—	—	—	—	—
Vanellus vanellus pullus	—	—	—	—	—	—	—	—	—	—

Prey remnants (r), pellets (p) and casual field observations (f)												
Ameland	Flevoland			Gr. Peel			N. France			S. France		
1970	1971			1965			1970			1969		
f	r	p	f	r	p	f	r	p	f	r	p	f
—	—	—	—	—	—	—	—	1	—	—	3	—
—	—	—	—	—	—	—	—	—	—	38?	—	—
—	—	—	—	—	—	—	—	—	—	3	—	1
—	—	—	—	—	—	—	—	—	—	3	—	—
—	—	—	—	—	—	—	—	5	—	4	2	3
—	—	—	—	—	—	—	—	—	—	62	53	51
—	—	—	—	—	—	—	—	—	—	4	—	7
—	2	—	1	—	—	1	—	—	—	—	—	—
—	—	5	—	—	—	—	2	2	—	—	—	3
—	2	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	3	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	2	—	—	—	—	—	—	1	—	—	—
—	—	—	—	—	—	—	—	—	2	1	10	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	3	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	2	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—	1
—	—	—	—	—	—	—	5	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	5	3
—	1	—	—	—	—	—	—	—	—	2	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	17	16	3	—	—	—	1	—	—	—	—	—
—	1	1	—	—	—	—	—	—	—	1	2	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—

Appendix 2: Prey numbers observed in *Circus aeruginosus* (continued).

	Nest observations									
	Ameland	Terschelling	Flevoland			N. France		S. France		
	1964	1959	1971			1970		1969		
	1♀	1♂ + 1♀	2♂♂	2♀♀	Σ	1♀	1♂ + 1♀	3♂♂	2♀♀	Σ
Tringa totanus pullus	—	5	—	—	—	—	—	—	—	—
Philomachus pugnax adult	—	—	—	—	—	—	—	—	—	—
Recurvirostra avocetta adult	—	—	—	—	—	—	—	—	—	—
Nidifugous bird pullus	—	—	—	—	—	—	—	—	—	—
Passeriformes pullus	—	—	4	—	4	5	5	13	—	13
Passeriformes juvenile/adult	—	—	3	—	3	8	8	—	—	—
Passeriformes	—	—	—	—	—	—	—	—	—	—
Anthus/*Alauda* species	—	1	—	—	—	—	—	—	—	—
Alauda arvensis juvenile/adult	—	—	2	—	3	—	—	—	—	—
Alauda arvensis pullus	—	—	—	—	—	1	1	—	—	—
Motacilla flava	—	—	—	—	—	—	—	—	—	—
Turdus species	—	—	—	—	—	—	—	—	—	—
Turdus merula	—	—	—	—	—	—	—	—	—	—
Emberiza calandra	—	—	—	—	—	—	—	—	—	—
Emberiza schoeniclus	—	—	—	—	1	—	—	—	—	—
Carduelis species	—	—	—	—	—	—	—	—	—	—
Carduelis cannabina pullus	—	—	—	—	—	—	1	—	—	—
Carduelis cannabina juv./ad.	—	—	—	—	—	—	—	—	—	—
Pyrrhula pyrrhula, female	—	—	—	—	—	—	—	—	—	—
Passer domesticus	—	—	—	—	—	—	—	—	—	—
Sturnus vulgaris juvenile	1	—	—	—	—	1	1	—	—	—
Sturnus vulgaris	—	—	—	—	—	—	—	—	—	—
Pica pica pullus	—	—	—	—	—	—	—	—	—	—
Phylloscopus species pullus	—	—	—	—	—	—	—	—	—	—
Large mammal	—	—	—	—	—	1	2	—	—	—
Mammal unknown	—	—	—	—	—	—	—	—	—	—
Crocidura species	—	—	—	—	—	—	—	—	—	—
Talpa europaea	—	—	—	—	—	—	—	—	—	1
Rodentia	—	—	—	—	—	—	—	—	—	—
Lagomorpha	—	—	—	—	—	—	—	—	—	—
Lepus capensis	—	—	—	—	1	—	—	—	—	—
Oryctolagus cuniculus	10	12	4	1	10	—	—	32	5	61

Prey remnants (r), pellets (p) and casual field observations (f)												
Ameland	Flevoland			Gr. Peel			N. France			S. France		
1970	1971			1965			1970			1969		
f	r	p	f	r	p	f	r	p	f	r	p	f
—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—
5	—	1	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—
—	3	2	—	—	+	—	9	4	—	—	4	—
9	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	2	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	3	—	—	4	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	5	—	—	—	—	—
—	—	—	—	—	—	—	4	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	2	—
—	1	1	—	1	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	2	1	—	—	—	—
—	—	—	—	—	—	—	—	—	—	2	—	2
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	+	1	—	—	—	—	3
—	—	—	—	—	—	—	—	3	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	4	—
—	—	18	—	—	—	—	—	1	—	—	48	—
—	1	—	—	—	—	—	—	—	—	—	—	—
+	26	—	4	—	—	—	5	—	—	49	—	12

Appendix 3: Prey numbers observed in *Circus aeruginosus* (continued).

	Nest observations									
	Ameland	Terschelling	Flevoland			N. France		S. France		
	1964	1959	1971			1970		1969		
	1♀	1♂ + 1♀	2♂♂	2♀♀	Σ	1♀	1♂ + 1♀	3♂♂	2♀♀	Σ
Clethrinomys glareolus	—	—	—	—	—	—	—	—	—	—
Arvicola terrestris	—	—	—	—	—	—	—	—	—	—
Arvicola amphibius	—	—	—	—	—	—	—	—	—	—
Microtus arvalis	—	—	1	—	3	—	—	—	—	—
Micromys minutus	—	—	4	—	4	—	—	—	—	—
Sylvaemus sylvaticus	—	1	—	—	—	—	—	—	—	—
Rattus norvegicus young	—	—	—	—	—	—	—	6	—	8
Rattus norvegicus adult	—	—	—	—	—	—	—	2	—	5
Ondathra zibethicus	—	—	—	—	—	—	—	—	—	—
Mouse or vole	—	—	—	—	—	—	—	—	—	—
Circus aeruginosus pullus	—	—	—	1	1	—	—	—	—	—
Larus ridibundus pullus	—	—	—	—	—	—	—	—	—	—
Larus ridibundus juvenile/adult	—	—	—	—	—	—	—	—	—	—
Chlidonia species	—	—	—	—	—	—	—	—	—	—
Columbidae	—	—	—	—	—	—	—	—	—	—
Cuculus canorus juvenile	—	—	—	—	—	—	—	—	—	—
Apus apus	—	—	—	—	—	—	—	—	—	—
Unknown birds	5	—	2	1	5	—	—	1	—	1
Bird eggs	—	—	—	—	—	—	—	—	—	—
Carrion	—	—	—	—	—	—	—	—	—	—
Unknown	1	1	1	—	1	1	1	—	2	6

Prey remnants (r), pellets (p) and casual field observations (f)												
Ameland	Flevoland			Gr. Peel			N. France			S. France		
1970	1971			1965			1970			1969		
f	r	p	f	r	p	f	r	p	f	r	p	f
—	—	—	—	—	+	—	—	—	—	—	—	—
—	—	—	—	1	—	—	1	3	—	—	—	—
—	—	—	—	—	+	—	—	—	—	1	2	—
—	—	—	—	—	+	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	2
—	1	—	—	—	—	—	—	—	—	2	2	2
—	—	—	—	—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	6	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	+	—	—	—	—	—	—
—	—	—	—	6	—	+	—	—	—	1	—	1
—	—	—	—	—	—	—	—	—	—	2	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	1	2	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	2	—
—	—	1	—	—	—	—	2	1	—	3	14	1
—	—	6	—	—	—	+	—	—	—	—	1	2
—	—	—	2	—	—	—	—	—	—	2	—	—
—	—	—	93	—	—	—	—	1	33	—	—	106

Appendix 4: Prey numbers observed in *Circus cyaneus.*

	Nest												
	Ameland							Terschelling					
	1964	1967			1970			1959	1961	1962	1968		
	1♂ + 1♀	3♂♂	4♀♀	Σ	2♂♂	3♀♀	Σ	1♂ + 1♀	1♂ + 1♀	3♂♂ + 3♀♀	3♂♂	4♀♀	Σ
Lizard	—	—	—	—	—	—	—	—	—	—	—	1	1
Anas species pullus	—	—		—	—	1	1	—	—	—	—	—	—
Spatula clypeata		—	—	—	—	1	1	—	—	—	—	—	—
Tadorna tadorna pullus	—	—	—	—	—	—	—	—	—	—	1	2	3
Gallinula cholropus pullus . . .	—	—	4	4	1	3	4	—	—	—	—	—	—
Gallinula chloropus juvenile . . .	—	—	—	—	—	—	—	—	—	—	—	—	—
Fulica atra pullus	—	—	1	1	1	—	1	—	—	—	—	—	—
Perdix perdix pullus	—	—	1	1	1	—	1	—	—	—	—	—	—
Perdix perdix adult	—	—	—	—		—	—	—	—		—	—	—
Coturnix coturnix adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Phasianus colchicus pullus/juvenile .	2	6	20	26	2	17	19	—	7	5	—	—	—
Limicolae pullus	—	11	9	20	6	9	15	—	—	—	2	4	6
Limicolae	—	—	—	—	—	—	—	—	—	—	—	—	—
Haematopus ostralegus pullus . .	—	—	3	3	2	2	4	2	—	—	1	1	2
Vanellus vanellus pullus	—	2	—	2	—	1	1	—	1	—	—	3	3
Charadrius species pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Charadrius species adult . . .	—	—	—	—	—	—	—	—	—	—	—	—	—
Numenius arquata pullus	—	—	2	2	3	7	10	—	—	2	—	—	—
Limosa limosa pullus	—	—	—	—	—	—	—	—	—	3	—	—	—
Tringa totanus pullus	—	2	—	2	1	1	2	—	—	—	—	—	—
Passeriformes pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Passeriformes juvenile/adult . . .	—	—	—	—	—	—	—	—	—	—	—	—	—
Passeriformes	8	25	19	44	12	4	16	7	31	19	1	11	12
Anthus/Alauda species	7	2	2	4	—	—	—	20	72	44	7	5	12
Alauda arvensis pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Alauda arvensis juvenile/adult . .	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthus pratensis pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthus pratensis juvenile/adult . .	—	—	—	—	—	—	—	—	—	—	—	—	—
Motacilla alba	—	—	—	—	1	—	1	—	—	—	—		—
Motacilla flava	—	—	—	—	—	—	—	1	1	—	—	—	—
Lanius collurio	—	—	1	1	—	—	—	—	—	—	—	—	—

observations						Prey remnants (r), pellets (p) and casual field observations (f)									
Flevoland						Terschelling			Flevoland				N. France		
1971			1972			1959	1961	1962	1971			1972	1970		
2♂♂	2♀♀	Σ	2♂♂	2♀♀	Σ	f	r	r	r	p	f	r	r	p	f
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
3	2	6	29	11	49	—	1	1	1	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	—	3	1	—	1	—	—	—	—	—	—	—	—	—	—
9	1	10	2	3	5	—	—	—	—	14	—	1	—	2	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—
3	—	3	—	—	—	—	1	2	2	—	—	1	—	—	—
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Appendix 5: Prey numbers observed in *Circus cyaneus* (continued).

	Nest													
	Ameland							Terschelling						
	1964	1967			1970			1959	1961	1962	1968			
	1♂ + 1♀	3♂♂	4♀♀	Σ	2♂♂	3♀♀	Σ	1♂ + 1♀	1♂ + 1♀	3♂♂ + 3♀♀	3♂♂	4♀♀	Σ	
Oenanthe oenanthe	1	—	1	1	—	—	—	—	—	2	—	—	—	
Saxicola rubetra	3	—	—	—	—	—	—	2	—	6	—	—	—	
Locustella naevia	—	—	—	—	1	—	1	—	—	—	—	—	—	
Acrocephalus scirpaceus	—	—	—	—	—	—	—	—	—	—	—	—	—	
Acrocephalus schoenobaenus	—	—	—	—	—	—	—	—	1	—	—	—	—	
Sylvia communis	—	—	—	—	4	—	4	2	3	2	—	—	—	
Phylloscopus trochilus	—	6	3	9	5	—	5	—	12	1	—	—	—	
Parus major	—	—	1	1	—	—	—	—	—	—	—	—	—	
Panurus biarmicus	—	—	—	—	—	—	—	—	—	—	—	—	—	
Emberiza citrinella	—	—	—	—	—	—	—	—	—	—	—	—	—	
Emberiza schoeniclus	1	—	1	1	—	1	1	—	5	4	—	—	—	
Carduelis cannabina	—	—	—	—	—	—		—	—	3	—	—	—	
Sturnus vularis juvenile	—	—	—	—	—	—	—	—	—	—	—	—	—	
Sturnus vulgaris adult	—	—	—	—	—	—	—	—	—	—	—	—		
Sturnus vulgaris	9	1	2	3	1	—	1	—	9	1	—	—	—	
Unknown mammal	—	—	—	—	—	—	—	—	—	—	—	—	—	
Neomys fodiens	—	—	—	—	—	—	—	—	—	—	—	—	—	
Lagomorpha	—	—	—	—	—	—	—	—	—	—	—	—	—	
Oryctolagus cuniculus	2	4	27	31	5	17	22	12	19	48	3	15	18	
Mouse or vole	—	—	—	—	—	—	—	—	—	—	—	2	2	
Vole	—	—	—	—	—	—	—	—	—	—	—	—	—	
Microtus arvalis	—	8	7	15	2	—	2	—	—	—	—	—	—	
Micromys minutus	—	—	—	—	—	—	—	—	—	—	—	—	—	
Sylvaemus sylvaticus	—	1	—	1	1	—	1	—	1	—	—	—	—	
Mouse or rat	—	3	1	4	—	—	—	—	—	—	—	—	—	
Rattus norvegicus	—	—	1	1	—	—	—	—	—	—	—	—	—	
Columba palumbus	—	—	—	—	—	1	1	—	—	—	—	—	—	
Unknown birds	7	—	—	—	—	—	—	—	—	—	—	—	—	
Unknown	2	9	8	17	3	5	8	—	—	5	—	—	—	

observations						Prey remnants (r), pellets (p) and casual field observations (f)									
Flevoland						Terschelling			Flevoland				N. France		
1971			1972			1959	1961	1962	1971			1972	1970		
2♂♂	2♀♀	Σ	2♂♂	2♀♀	Σ	f	r	r	r	p	f	r	r	p	f
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
1	—	1	2	—	2	—	—	1	2	—	—	1	1	—	—
1	—	1	—	—	—	—	1	2	—	—	—	—	—	—	—
3	2	5	1	2	3	—	1	1	3	—	—	—	—	—	—
4	5	10	—	—	—	—	—	—	—	2	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	11	—	—	—	—	—
—	2	4	—	5	6	1	—	—	—	—	1	3	—	—	—
2	—	2	—	—	—	—	—	—	—	—	1	—	—	—	—
3	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—
8	3	11	—	—	—	—	—	—	—	8	—	—	—	—	—
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	3	—	—	—	—	1	1	—	—	—	—
1	1	2	1	—	2	—	—	—	—	—	26	—	—	—	5

Appendix 6: Prey numbers observed in *Circus pygargus*.

	Nest												
	Ameland							Terschelling					
	1964	1967			1970			1959	1961	1962	1968		
	1♂ 1♀	2 ♂♂	2 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ	2 ♂♂ 2 ♀♀	1♂ 1♀	2 ♂♂ 2 ♀♀	1♂	1♀	Σ
Tettigonia species (Orthoptera)	—	—	—	—	—	—	—	2	—	—	—	—	—
Odonata	—	—	—	—	—	—	—	—	—	—	—	—	—
Large insects	—	—	—	—	—	—	—	1	—	—	—	—	—
Frog	—	—	—	—	—	—	—	1	—	—	—	—	—
Lizards	—	—	—	—	—	—	—	65	85	143	—	1	1
Anas species pullus	—	—	—	—	—	1	1	—	—	—	—	—	—
Tadorna tadorna pullus	—	—	1	1	1	—	1	—	—	—	—	—	—
Gallinula chloropus pullus	—	—	3	3	—	—	—	—	—	—	—	—	—
Fulica atra pullus	—	—	—	—	—	2	2	—	—	—	—	—	—
Perdix species pullus	—	—	1	1	—	—	—	—	—	—	—	—	—
Phasianus colchicus pullus/juvenile	—	—	—	—	15	3	18	—	—	—	—	—	—
Limicolae pullus	1	4	2	6	3	—	3	—	3	—	1	1	2
Limicolae	—	—	—	—	—	—	—	—	—	—	—	—	—
Haematopus ostralegus pullus	1	—	—	—	1	—	1	—	—	—	1	1	2
Vanellus vanellus pullus	—	—	—	—	—	—	—	2	1	2	—	—	—
Charadrius species pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Charadrius species adult													
Numenius arquata pullus	—	—	—	—	2	—	2	—	—	—	1	—	1
Limosa limosa pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Tringa totanus pullus	—	—	—	—	—	—	—	—	—	1	—	—	—
Philomachus pugnax adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Recurvirostra avocetta pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Nidifugous bird pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Passeriformes pullus	—	—	—	—	—	—	—	7	—	—	—	—	—
Passeriformes juvenile/adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Passeriformes	26	13	12	25	16	3	19	9	12	17	4	9	13
Anthus/*Alauda* species pullus	—	—	—	—	—	—	—	10	—	—	—	—	—
Anthus/*Alauda* species	17	11	5	16	—	—	—	45	70	59	1	3	4
Alauda arvensis pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Alauda arvensis juvenile/adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Hirundo rustica	—	—	—	—	—	—	—	—	—	—	—	—	—

observations									Prey remnants (r), pellets (p) and casual field observations (f)												
Flevoland			Gr. Peel			S. France			Terschelling			Gr. Peel		Flevoland			N. France		S. France		
1971			1965			1969			1959	1961	1962	1965		1971			1970		1969		
2 ♂♂	2 ♀♀	Σ	1♂	1♀	Σ	2 ♂♂	2 ♀♀	Σ	f	r	r	r	p	r	p	f	r	f	r	p	f
—	—	—	—	—	—	9	51	63	—	—	—	—	—	—	—	—	2	—	2	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
—	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	9	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	2	1	3	1	—	—	—	—	—	—	—	—	—	—	2	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	4	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—
3	1	5	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
11	1	14	6	3	9	—	—	—	4	—	—	—	—	3	—	1	—	—	—	—	—
3	2	5	15	1	16	8	3	12	3	—	—	—	9	2	37	1	2	—	1	23	—
1	1	2	—	—	—	—	—	—	—	1	—	—	—	—	2	—	—	—	—	—	—
—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	3	1	4	—	—	—	—	—	—	—	—	—	—	1	—	—
13	1	14	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
6	1	7	6	—	7	—	—	—	—	4	4	—	—	17	2	2	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—

Appendix 7: Prey numbers observed in *Circus pygargus* (continued).

	Nest												
	Ameland							Terschelling					
	1964	1967			1970			1959	1961	1962	1968		
	1 ♂ 1 ♀	2 ♂♂	2 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ	2 ♂♂ 2 ♀♀	1 ♂ 1 ♀	2 ♂♂ 2 ♀♀	1 ♂	1 ♀	Σ
Anthus species juvenile	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthus pratensis juvenile/adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Motacilla alba juvenile	—	—	—	—	—	—	—	—	—	—	—	—	—
Motacilla alba	—	—	—	—	—	—	—	1	—	—	—	—	—
Motacilla flava		—	—	—	—	—	—	1	—	—	—	—	—
Motacilla species	1	—	—	—	—	—	—	—	—	—	—	—	—
Turdus species pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Turdus merula pullus	—	—	—	—	—	—	—	—	—	—	—	—	—
Saxicola rubethra	—	—	—	—	—	—	—	—	—	2	—	—	—
Locustella naevia	—	—	—	—	—	—	—	—	—	—	—	—	—
Acrocephalus schoenobaenus	1	—	—	—	—	—	—	—	—	—	—	—	—
Sylvia communis	—	—	—	—	1	—	1	1	—	—	—	—	—
Emberiza calandra	—	—	—	—	—	—	—	—	—	—	—	—	—
Emberiza citrinella	—	—	—	—	—	—	—	—	—	—	—	—	—
Emberiza schoeniclus juvenile/adult	—	—	—	—	—	—	—	—	—	—	—	—	—
Emberiza schoeniclus	3	—	—	—	12	—	12	—	—	3	—	—	—
Carduelis cannabina	—	—	—	—	4	—	4	—	2	—	—	—	—
Fringilla coelebs	—	—	—	—	1	—	1	—	—	—	—	—	—
Passer domesticus	—	—	—	—	—	—	—	—	—	—	—	—	—
Passer montanus	—	—	—	—	—	—	—	—	—	—	—	—	—
Sturnus vulgaris juvenile	—	—	—	—	—	—	—	—	—	—	1	—	1
Sturnus vulgaris	3	—	—	—	1	—	1	—	—	3	—	—	—
Micromys minutus	—	—	—	—	—	—	—	1	—	—	—	—	—
Soricidae	—	—	—	—	—	—	—	—	—	2	—	—	—
Lagomorpha	—	—	—	—	—	—	—	—	—	—	—	—	—
Oryctolagus cuniculus	1	—	2	2	4	—	4	—	—	1	—	—	—
Clethrionomys glareolus	—	—	—	—	—	—	—	—	—	—	—	—	—
Arvicola terrestris	—	—	—	—	—	—	—	—	—	—	—	—	—
Mouse or vole	13	—	—	—	—	1	1	—	—	—	—	3	3
Vole	—	—	—	—	—	—	—	—	—	—	—	—	—

observations									Prey remnants (r), pellets (p) and casual field observations (f)												
Flevoland			Gr. Peel			S. France			Terschelling			Gr. Peel		Flevoland			N. France		S. France		
1971			1965			1969			1959	1961	1962	1965		1971			1970		1969		
2 ♂♂	2 ♀♀	Σ	1 ♂	1 ♀	Σ	2 ♂♂	2 ♀♀	Σ	f	r	r	r	p	r	p	f	r	f	r	p	f
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
1	—	1	3	—	3	—	—	—	—	4	4	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	1	—	—	—	—	—	—	—	2	—	—	5	2	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	1	1	—	—	—	—	2	—	1	2	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	5	—	5	—	—	—	1	1	—	—	—	—	—	—	—	2
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—
2	2	4	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—
—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	2	2	—	—	—	—	16	—	10	—	—	—	—	2	—
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1

	Nest												
	Ameland							Terschelling					
	1964	1967			1970			1959	1961	1962	1968		
	1 ♂ 1 ♀	2 ♂♂	2 ♀♀	Σ	2 ♂♂	2 ♀♀	Σ	2 ♂♂ 2 ♀♀	1 ♂ 1 ♀	2 ♂♂ 2 ♀♀	1 ♂	1 ♀	Σ
Microtus arvalis	—	5	18	23	5	—	5	—	—	—	—	—	—
Sylvaemus sylvaticus	—	—	1	1	—	—	—	9	5	7	—	—	—
Mouse or rat	—	9	19	28	—	—	—	—	—	—	—	—	—
Rattus norvegicus young	—	—	1	1	—	—	—	—	—	—	—	—	—
Circus pygargus pullus	1	—	—	—	—	—	—	—	—	—	—	—	—
Cuculus canorus juvenile	—	—	—	—	—	—	—	—	—	—	—	—	—
Unknown bird	—	—	—	—	—	—	—	—	—	—	—	—	—
Bird eggs	—	—	—	—	—	—	—	—	—	—	—	—	—
Unknown	6	15	25	40	3	2	5	16	—	8	—	—	—

observations									Prey remnants (r), pellets (p) and casual field observations (f)															
Flevoland			Gr. Peel			S. France			Terschelling			Gr. Peel		Flevoland			N. France		S. France		
1971			1965			1969			1959	1961	1962	1965		1971			1970		1969		
2 ♂♂	2 ♀♀	Σ	1♂	1♀	Σ	2 ♂♂	2 ♀♀	Σ	f	r	r	r	p	r	p	f	r	f	r	p	f
6	—	6	2	—	2	—	—	—	—	—	—	—	—	1	4	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
1	—	1	4	—	4	—	—	—	—	—	—	—	—	—	4	1	—	2	1	—	3
—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3	—	—	—	—	—	—
—	—	—	5	1	6	2	1	3	—	—	—	—	—	—	—	64	—	14	—	—	32

Appendix 8: Estimated weights of prey.

	Prey species, numbered according to prey categories	weight (g)
1.	Large insect	1.5
2.	Fish	150
3.	Frog	20
4.	Snake	120
5.	Lizard	10
6.	*Anas* species pullus	75
	Anas platyrhynchos pullus	100
	Spatula clypeata pullus	50
	Somateria mollissima pullus	100
	Tadorna tadorna pullus	100
	Rallidae pullus	75
	Rallus aquaticus pullus	40
	Gallinula chloropus pullus	75
	Fulica atra pullus	125
7.	*Anas* species adult	675
	Anas species juvenile	300
	Anas platyrhynchos adult	1 040
	Anas platyrhynchos juvenile	700
	Anas crecca adult	310
	Rallidae adult	300
	Rallus aquaticus adult	110
	Gallinula chloropus adult	249
	Gallinula chloropus juvenile	170
	Fulica atra juvenile	425
8.	*Perdix* species pullus	50
	Perdix species adult	400
	Phasianus colchicus pullus	50
	Phasianus *colchicus*, larger	100
	Phasianus colchicus, half grown	500
	Limicolae pullus	75
	Haematopus ostralegus pullus	100
	Vanellus vanellus pullus	50
	Charadrius species pullus	20
	Numenius arquata pullus	100
	Limosa limosa pullus	80
	Tringa totanus pullus	40
	Recurvirostra avocetta pullus	50
	Nidifugous bird pullus	60
9.	Passeriformes pullus	17
	Passeriformes juv. or ad.	25
	Anthus/Alauda species pullus	21
	Anthus/Alauda species juv./ad.	29
	Alauda species juv./ad.	35
	Alauda arvensis pullus	22
	Alauda arvensis juv./ad.	35
	Anthus species juv./ad.	19
	Anthus pratensis pullus	14
	Anthus pratensis juv./ad.	19
	Motacilla alba	22
	Motacilla flava	17
	Lanius collurio	33
	Turdus species	60
	Turdus merula pullus	60
	Turdus merula adult	95
	Oenanthe oenanthe	26
	Saxicola rubethra	18
	Locustella naevia	14
	Acrocephalus scirpaceus	13
	Acrocephalus schoenobaenus	12
	Sylvia communis	14
	Phylloscopus trochilus	9
	Parus major	19
	Panurus biarmicus	15
	Emberiza calandra	54
	Emberiza citrinella	29
	Emberiza schoeniclus pullus	14
	Emberiza schoeniclus juv./ad.	19
	Carduelis species	18
	Carduelis cannabina pullus	12
	Carduelis cannabina juv./ad.	18
	Fringilla coelebs	22
	Passer domesticus	30
	Passer montanus	24
	Sturnus vulgaris	78
	Pica pica pullus	120
10.	Soricidae	10
	Sorex minutus	5
	Clethrionomys glareolus	25
	Mouse	25
	Vole	25
	Microtus arvalis	25
	Micromys minutus	10
	Apodemus sylvaticus	25
	Mouse, vole or rat	50
	Rattus norvegicus young	100
	Mus domesticus	25
11.	Larger mammal	250
	Talpa europaea	100
	Oryctolagus/Lepus young	250
	Arvicola terrestris	150
	Rattus norvegicus	300
12.	*Circus aeruginosus* pullus	120
	Circus pygargus pullus	100

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