



GUSTAF RUDEBECK

**The choice of prey and modes
of hunting of predatory birds with special reference
to their selective effect**

This work is a reprint of two papers that originally appeared in Oikos. The author and Oikos have given their kind permission to the Ornithological Society of Skåne to make this reprint.

This work should be quoted as:

Rudebeck, G. 1950-51. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. -
Oikos 2: 67-88, 3: 200-231.

Omslagsteckning av Allan Andersson



ANSER
Supplement nr 10

Contribution No. 75 from Falsterbo Bird Station

THE CHOICE OF PREY AND MODES OF HUNTING OF PREDATORY BIRDS WITH SPECIAL REFERENCE TO THEIR SELECTIVE EFFECT

BY

GUSTAF RUDEBECK

(*Zoological Institute, Lund.*)

The literature on the food of the North-European birds of prey is at present fairly extensive. Among older works should be mentioned RÖRIG, 1909, among more recent publications GROEBBELS, 1932, and especially URTENDÖRFER, 1930, 1931, and 1939. FERDINAND (1923) has made a contribution from Denmark, and HAGEN (1948) has lately published an investigation from Norway. In recent years fairly comprehensive studies of the hunting methods of predatory birds have also been made in connection with the increased interest in ecological questions. TINBERGEN (1946) has thus described the hunting methods and choice of prey of the sparrow-hawk (*Accipiter nisus*) at some length. He has also investigated the significance of this bird as a mortality factor (regulator) for certain species of small birds. — Good descriptions of the modes of hunting of birds of prey are also found in many modern ornithological handbooks (NIETHAMMER, 1938; TUCKER in WITHERBY et al., 1945; ROSENBERG in HOLMSTRÖM et al., 1944, among others). Much remains, however, to be done in this field. Only very few species have been subjected to close investigation, and I am firmly convinced that thorough observations, correctly interpreted, of the behaviour of living animals will always yield valuable results even when zoological science has become more advanced than it is today.

Present day research on population dynamics carried out so intensively (see, for example, ELTON, 1942 and KALELA, 1949), obviously has points in common with the investigations on the selection of prey of predatory birds. LACK (1946) has discussed the competition among various species of birds of prey for food. Finally, some authors have directly studied the question of "the relationship between predator and prey", for instance BODENHEIMER, 1938, OMER-COOPER, 1948, and others.

It would be very easy to enlarge the list of publications which, like those

cited above, treat the relationship between predator and prey from a quantitative point of view. If, as in this paper, we instead lay the main stress on the qualitative point of view and seek a possible selective effect of the choice of prey of predatory birds, the literature on that subject is comparatively sparse. The question could hardly be raised at all until the doctrine of evolution had been accepted and the struggle for existence and selection were introduced as explanations of the development. Nor could an answer to the question be expected until a thorough investigation of the ecology of both predators and their prey had been made, and particularly of the mutual ecological relationships between these two groups of animals. During the last fifty years the problem has been treated with interest in many different connections, but the lack of applicable primary material seems to have been universal and is largely responsible for the limited debate on this subject.

Formulation of the problem

The question of whether the choice of prey of predatory birds has a selective effect can also be expressed as follows: Are the individuals selected by predatory birds chosen at random from the population? In other words: when a bird of prey attacks a certain quarry, why is that particular individual pursued and killed? Did it possess any special quality in which it differed from other members of its own kind? If so, what was that quality?

Thus, the problem is not which species of animals serve as food to the various birds of prey, but which individuals that are killed. The qualitative viewpoint and not the quantitative one should be emphasized, although these two sides of the matter are not completely independent of each other (cf. the selective effect in populations of various size, WRIGHT, 1931, 1940).

The answers to the questions formulated cannot be obtained from analyses of remains of the quarry, pellets, and the like, at least not by such methods alone. We must also have a great number of observations on the hunting of predatory birds, not only their modes of hunting but also the percentage of successful hunts, the normal reactions of the various species to predators, the behaviour of the chased animals, possible deviations in some respect or other from normal behaviour, etc. Of particular interest is the question whether the specimens which are abnormal in any respect fall a victim to predatory birds comparatively often. Accidental occurrences and false deductions due to insufficient material must be avoided. Since individual specimens of birds of prey may specialize on a certain quarry (prey) or mode of hunting (NIETHAMMER, 1938; UTTENDÖRFER, 1939; TINBERGEN, 1946; my own observations) it is desirable that observations are gathered from as many

specimens of hunting birds as possible. The investigations, therefore, cannot be based solely on a study of a few pairs of breeding birds of prey. If any conclusions are to be drawn, the hunting of the bird of prey must be followed closely, preferably from the beginning to the end, and the behaviour of both predator and prey must be studied and noted.

Extremely divergent opinions are known to have been advanced as to the function of the bird of prey in nature. Man's primitive hostile attitude towards these animals still survives in wide circles, not only among primitive people but also among hunters who belong to the so-called civilized peoples. This attitude is, of course, very interesting from many points of view but has very little to do with scientific research and will therefore not be discussed here. The question has been treated previously in another connection (RUDEBECK, 1949).

*

The discussion of the selective effect of birds of prey started in the decades when the idea of their "destructiveness" was most deeply rooted and the birds were pursued with frantic energy. It is interesting to review the arguments presented against the ruling opinion in the beginning of the twentieth century. OBERLÄNDER (1907), for example, considers that the extirpation of predators had disastrous effects on wild game. He says *inter alia*: "Sick or crippled birds are of far more interest to predators than healthy animals. If a goshawk or peregrine falcon swoops down upon a flock of game birds, one of which is crippled, the latter is taken first. I have observed this to happen so often that there can be no question of coincidence. Predatory birds know from experience that a sick bird is their easiest prey and they notice the sick animals at once from their movements, carriage, and ruffled feathers." (Orig. German.)

SCHÄFER (1938) who evidently had a wide experience from the field, says of the Bearded Vulture (*Gypaëtus barbatus*): "Kranke Herdentiere kann er mit Sicherheit von gesunden Stücken unterscheiden". The same author gives also several examples on how specimens of *Aquila rapax* with extraordinary swiftness attack and seize wounded birds which are just falling down. In his opinion this is "another proof that the large raptorial birds immediately and infallibly attack and kill sick game, while healthy animals usually escape".

DURANGO (1948) on three occasions has seen sparrow-hawks (*Accipiter nisus*) seize, out of large flocks of small birds, the particular specimen that he knew was physically defective. He draws the conclusion that this cannot be mere coincidence.

KRAMER, one of UTTENDÖRFER's co-workers (see UTTENDÖRFER, 1931) was able to demonstrate that the racing pigeons that had fallen victims to peregrine falcons, largely consisted of stray individuals. UTTENDÖRFER surmises, probably quite correctly, that such specimens are particularly easy to catch.

BRINKMANN (1923, 1927) has maintained with acerbity and exhaustive argumentation the significance of predatory birds as "sanitary police". He discusses the question in connection with his wellknown studies of coccidiosis in willow grouse (*Lagopus lagopus*) in Norway. He argues as follows (1927, p. 47—49): "It is justifiable to assume that a predatory bird seeks its prey where it is most easily taken. Birds of prey do not hunt for sport. Since we know that sick grouse do not take cover or fly very far, it is legitimate to conclude that birds of prey prefer to seize sick animals. They will thereby have a sanitary effect on the stock." This theory is strongly supported by I. B. BARTH (1894) who is quoted by BRINKMANN. BARTH says he has observed on many occasions that gyrfalcons and peregrine falcons notice at once if there is a crippled individual among frightened grouse; this specimen is then always selected.

BRINKMANN's account (l. c. p. 62—63) of the consequences of the energetic persecution of birds of prey is very interesting: "The result of the decimation of birds of prey was a perfectly enormous increase in the stock of willow grouse, which culminated in 1911. It was then larger than it had ever been before. But as no attempt had been made to preserve the stock by having game keepers to collect sick and dead game and to cleanse . . . infected areas . . ., the result was a complete collapse of the stock, which became the prey of a violent epizootic (coccidiosis), which, because the coveys in the large stock lay very close together in the summer, had quite exceptionally favourable conditions for development. The epizootic has continued year after year with small deviations, and it is obvious that it was not checked until the stock was very much reduced. The coveys then lay so far apart during the breeding season that the danger of infection was reduced considerably thereby."

An essential contribution to the question of selection is also LORENZ' highly interesting and astute treatise "Die angeborenen Formen möglicher Erfahrung" (1943). LORENZ discusses at some length the consequences of domestication for domestic animals and stresses strongly the degeneration, both psychic and physical, which results when a species through domestication is withdrawn from the effects of natural selection.

LORENZ worked with wild and tame specimens of several species including the greylag (*Anser anser* (L)). These two stocks showed very great differences in survival capacity when placed in the same environment. The figures may

be quoted: During the winter of 1939—40 the author had in his research station 41 greylags, of which 27 were of pure wild stock and 14 cross-breeds between wild and tame birds. "Als nun die Gänse durch vorübergehenden Futtermangel, Zufrieren des Teiches und den Einbruch von Füchsen gezwungen wurden, fortzuziehen und kurze Zeit das Leben wilder Graugänse zu führen, verloren die Reinblüter (= the wild stock) nur 5 Vögel, alles diesjährige unerfahrene Junge . . ., während von den Mischblütern (= the cross production between wild and tame birds) 8 Tiere zugrunde gingen." In other words, the mortality rate for wild birds was 18.5 and for tame birds 57. LORENZ concludes that "die Wildform gegen die feindlichen Einwirkungen der ausserartgenössischen Umwelt um ein Vielfaches widerstandsfähiger ist als das stumpfsinnige, mit Ausnahme von Fressen und Begattung in allen seinen Verhaltensweisen reaktionsschwache Haustier". When the animals were kept enclosed and breeding was free the tame greylags and the progeny of tame \times wild birds increased much more rapidly than the pure wild stock. The conclusion is naturally that the tame greylags are "unendlich viel durchschlagskräftiger als die Wildform, wenn nicht äussere Umwelteinflüsse, sondern die Raumkonkurrenz der Artgenossen der einzige zu überwindende, die Vermehrung hindernde Faktor ist. Im Stalleben kommt es eben nicht darauf an, feinsinnig den Feind auf grosse Entfernung wahrzunehmen, seine Kinder mutig zu beschützen oder einen Gatten zu wählen, der diese Reaktionen in vollem Ausmass besitzt, sondern ausschliesslich darauf, mit möglichst grossem Appetit und möglichst geringer Selektivität wahllos und masslos zu fressen und zu zeugen! Deshalb entwickeln begreiflicherweise alle jene Verfallserscheinungen, die eine derartige Vereinfachung und 'Verrohung' des arteigenen Verhaltens bewirken, unter den Bedingungen des Haustierlebens einen stark positiven Auslesewert."

In summarizing one might say that many zoologists and geneticists are inclined to believe in the selective effect of predatory birds although they cannot often substantiate their opinion. Many authors (e. g. WESENBERG-LUND 1929, JÄGERSKIÖLD 1945) do not even try to confirm their views. Even the examples given above show the weak points in the argument. Those who have studied the predators in the field have generally not made any detailed records but have given general impressions and rules without being able to confirm them. LORENZ is one of the few who have published quantitative studies, but of course he could not report the causes of death in the various flocks of greylags. BRINKMANN's investigation is undoubtedly important but his views on the part played by predatory birds were largely based on indirect evidence and some bird-watchers quoted by him were, for various reasons, unreliable. Another weak point is that the various species of birds of prey are generally treated as a group instead of individually.

It also appears as if in recent years a more sceptical attitude towards the selective effect of predators has gained ground among geneticists and research workers on game. This is probably due partly to theoretical reflections on other causes of death in the stocks of game, chiefly the competition within the same species, and perhaps partly to the difficulties encountered in proving the other point of view. SVARDSON's comprehensive paper (1949) is a good example of this more sceptical attitude.

The influence of predators on game stocks has naturally been a common subject of discussion in game literature. The problem, if visualized clearly, has usually been formulated as follows: Do predatory birds preferably seize sick, injured or in other ways inferior game? Do birds of prey, in other words, serve as a kind of "sanitary police" for the game? In Swedish game literature these questions are often treated with open irony, which must be considered as hardly an adequate position, particularly in consideration of the standard of knowledge of the writers. Among sportsmen the answer is most often negative.

In another connection (RUDEBECK, 1949) I have discussed briefly the attitude of recent Swedish game literature towards the problem of predators. The main impression is that little new has been added from this quarter and that biased views, lack of objectivity, and lack of desire for objective treatment still flourish there. In recent years, however, several positive contributions have been published. The modern *Svenskt Jaktlexikon* [= Swedish Hunting Dictionary] (1947) shows remarkably often an evident unwillingness to make a declaration in the heated discussion concerning predators. It is quite objective with regard to some species; towards others, however, the old bitter attitude still exists and in order to justify this attitude even obviously misleading data are submitted, as in the case of the goshawk. Concerning some species of raptorial birds, it is "left to the individual hunter to decide whether he wishes to permit them on his grounds". The attitude of the sportsmen towards pertinent problems, as well as the game research which is carried out under the direction of the hunting clubs, seems to be in a period of transition.

Finally, a few words about the attitude of the conservationists towards these questions. They have, as a rule, defended predatory animals, believing them to have a beneficial effect, even from the stand-point of game preservation. Their main argument has been based on the classic Darwinian conception of "the survival of the fittest". The weak point of this reasoning is the lack of direct evidence due to insufficient observations. In my view, the opinion that no animal species should be outlawed, which is maintained by those interested in the protection of all organisms, should be treated with great respect. For purely scientific reasons, every animal species is of interest,

whether it is considered useful, injurious, or indifferent. It is utterly inexcusable simply to condemn any one animal species or — at best — to do so on the basis of our extremely imperfect knowledge of the synecology of the animals concerned. In so doing we greatly overestimate our present level of knowledge.

My own observations.

When LOWE in 1940 formed the question: "How do larger raptorial birds hunt their prey?", MEINERTZHAGEN (1940) made the following comment: "Mr Willoughby Lowe . . . has raised a question about which very little is known, mainly because no single person has been fortunate enough to witness more than a few instances". This fact probably explains why a large number of observations on the hunts of birds of prey have never been collected or, at least to my knowledge, never been published. I have, therefore, thought it justifiable to publish my own observations on this subject. They were collected and taken down during comprehensive ornithological field studies in southern Sweden during the period of 1935 to 1947; some notes date still further back. The observations from earlier years are, however, sparse and the annotations incomplete, particularly regarding unsuccessful hunts of predatory birds. Most observations — as well as the most thoroughly annotated ones — are for the years 1942—1945, when I resided in Falsterbo in the southwestern part of Sweden, about 55° 23' N and 12° 48' E, to study the autumn migration of birds. Field observations were also carried out in 1946 and 1947, at various places in Scania and Blekinge, and Ottenby on the southern point of Öland [where the bird observatory of the Ornithological Society of Sweden is located].

It should be pointed out that large numbers of migrating birds pass over southern Sweden every autumn, flying in a south-westerly direction. For bird migration at Ottenby, Öland, see SVÄRDSON 1948, 1949, 1950. In Skåne [Scania], especially at Falsterbo, the migrating birds are still more numerous, the most prominent groups being Corvidae, starling, finches, woodlarks, pipits, wagtails, pigeons, and birds of prey. The very marked concentration of migrating birds in Falsterbo in autumn is due to the form of the coast line where guiding lines converge towards Falsterbo [for the idea of guiding lines, see GEYR VON SCHWEPPENBURG 1929, 1933, 1936; for the autumn migration at Falsterbo, see VEDEL TANING 1931, RUDEBECK 1943, 1947, and 1950 (in press)].

I am fully aware that my observations are by no means perfect. They have, for instance, been made chiefly in Scania during autumn and winter. It would naturally be desirable to study the birds also in another environ-

ment and during other parts of the year, particularly in the breeding season. The area, however, had distinct advantages, and the observations collected have their merits, too. In many respects it is advisable to study the feeding habits of predatory birds during the autumnal migration. At that time of the year the supply of prey is largest; this is particularly true of the inexperienced young birds. It is evident from the ring-markings that the juvenile birds show a strikingly high mortality. One might therefore safely assume that predatory birds find it particularly easy to catch their prey during the autumnal migration. It should be kept in mind, however, that yearlings among the predators are also inexperienced and exposed to very great perils during their first year.

As mentioned before, many predatory birds specialize on a certain sort of prey, either because this quarry is especially abundant or because the individual bird has learned a particular mode of hunting which it has tried with success on one or more species of birds. The prey must naturally occur in a certain minimal frequency in order to become "favourised prey". One might therefore introduce a great source of error if only a small number of breeding pairs of predatory birds are studied. This source of error is avoided in observations of predatory birds on migration. Most specimens of predators, whose hunting methods and choice of prey I have investigated, have been migrants. I have only seen them hunt once or twice, and the next time both the bird of prey and its quarry have been new. In other words: from this point of view the material can be regarded as samples taken from an enormous population, which naturally is a great advantage.

The species examined

Since every animal species has its own ecological requirements the modes of hunting and the selective effect, if there is one, must obviously be examined for every species separately.

For several species of predatory birds, however, I do not possess a sufficient number of observations. Only in the case of four species is the material large enough to give significant results. The discussion will, therefore, only deal with these four species, namely:

Sparrow-hawk	<i>Accipiter nisus</i> (L.)
Merlin	<i>Falco columbarius</i> L.
Peregrine falcon	<i>Falco peregrinus</i> TUNST.
Sea-eagle	<i>Haliaeetus albicilla</i> (L.)

The three genera represent entirely different types of predatory birds. Even the two species of the genus *Falco* are not very closely related, be-

longing to different sub-genera and showing great differences in structure, size, and manner of living; they resemble each other in so far as they both prey mainly upon birds in flight.

All four species of predatory birds discussed in this paper have a very wide distribution (PETERS, 1931). *Accipiter nisus* occurs in the greater part of the palaearctic region, extending in winter into the adjacent southern regions. The species is divided into a number of subspecies: PETERS recognizes 10 forms, NIETHAMMER and WITHERBY only 6. In Sweden only *Accipiter nisus nisus* breeds; it occurs throughout most of the country. — The sparrowhawks which occur as passage-migrants in southern Sweden and undoubtedly breed in Finland and North Scandinavia, also belong exclusively to the nominate form, as far as is known (Förteckning över Sveriges fåglar 1949). Very closely related species exist in North and Central America.

Falco columbarius is a circumpolar and north-palaearctic species, breeding also in the arctic regions. It is a migratory bird and can be seen in winter as far south as the Caucasus, India, and Central America. Of its approximately 11 recognized forms only one occurs in Sweden, viz., *Falco columbarius aesalon* TUNSTALL; it breeds mainly in the northern and middle parts of the country (Förteckning över Sveriges fåglar 1949).

Falco peregrinus is practically cosmopolitan, breeding in all continents. Its geographical variation is considerable: PETERS recognizes 16 subspecies in all. As a rule (HARTERT, 1912—21; PETERS, 1931; SCHIÖLER, 1931; STEINBACHER in HARTERT-STEINBACHER 1932—1938; WITHERBY et al., 1945) the entire population of northern Europe is considered to belong to the nominate form, *Falco peregrinus peregrinus* TUNSTALL. The Förteckning över Sveriges fåglar (1949) mentions only this form for Sweden. Some authors, however, recognize slightly different subspecies in Great Britain, Germany, and Scandinavia (KLEINSCHMIDT 1913, 1916, and see discussion in HARTERT-STEINBACHER l. c.).

Haliaeetus albicilla, finally, is widely distributed in the palaearctic region and breeds also in the arctic zone. It has not been able to adapt itself to civilization to the same degree as the other three species mentioned, and has recently been exterminated by man in many countries and has become very rare in other countries, among them Sweden. The sea-eagle shows only slight geographic variation. SCHIÖLER (1931) considered it possible to separate a larger form from Greenland, but HARTERT (1912—21, p. 1178) and PETERS (1931) do not recognize any subspecies. The North-American *Haliaeetus leucocephalus* is very closely related, however, and, according to HARTERT and STEINBACHER (1932—38, p. 422), it can quite naturally be grouped together with *albicilla* in one "Rassenkreis".

From the foregoing it is evident that my observations refer to the nominate form except in the case of *Falco columbarius aesalon* TUNSTALL.

All four species of predatory birds in question have a very wide breeding area and are in some respects very slightly specialized, viz., they are not restricted to a certain kind of prey. With regard to structure, general ecology, and choice of prey they are very different, but all of them are obviously successful types.

The reactions of the predatory bird to its prey and vice versa.

Before proceeding to an examination of the various hunting methods and choice of prey of the different species, it is necessary to investigate the manner in which the predatory bird reacts towards its quarry and vice versa. I shall limit my discussion to the reactions between predatory birds and other *birds*, since most of my observations concern such cases. — Further it is essential to define a few terms concerning the hunting, attacking and search for prey of predatory birds.

a) On the sudden appearance of a predatory bird, other birds act in different ways. Those species which are quite out of the question as prey show no fright reaction whatsoever, or if they do, very soon calm down again. On the other hand, birds, for which the predatory bird is a potential danger, naturally try to escape the danger. In doing so they employ very different methods. Various species may behave in almost the same manner but specific reactions are also observed. The behaviour naturally varies with the type of predatory bird concerned, and also with the environment, season, distance to the bird, etc. A flight reaction of some kind is perhaps the most common occurrence. In some cases, however, the birds sit close together and in flying flocks they bunch together (literature and discussion by LORENZ, 1943, pp. 251—255; TINBERGEN, 1939). It is important to establish that the threatened animals usually observe the approaching raptorial bird in time and react in such a way as to make it impossible for the latter to seize a quarry; in most cases the predatory bird does not even make any attempt to attack, simply because it was discovered in time. This is undoubtedly the usual course of events. In suitable localities, where migrating birds concentrate in large numbers and where many birds of prey also pass, it happens so often that one cannot record every instance. If the bird does not hunt any specially selected individual (or flock of game), the case can naturally not be put down as hunting or attempted hunting.

b) Frequently a bird of prey is seen in flight, searching for quarry or at least prepared to attack if any quarry should appear. Since the bird is not hunting a certain individual, these cases, therefore, cannot be considered as instances of hunting.

We proceed now to the cases when a predatory bird really chases a certain

quarry or a flock, at least for a short moment. I have not investigated the problem from a psychological point of view, but it may be assumed that the bird of prey attacks when the quarry has a certain position in relation to the bird of prey. Perhaps one can also assume that the attack is released most surely and automatically, i. e., that the "desire to attack is strongest", at the moment when the quarry is in such a position that the chances of successful hunting are maximal. Birds of prey very often turn from migration flight to hunting if a suitable opportunity presents itself. This is particularly true of the sparrow-hawk, merlin, and peregrine falcon, but can also be said of sea-eagles, marsh harriers, and others. Buzzards (*Buteo* and *Pernis*), on the other hand, rarely break off their migratory flight in order to hunt, probably because they usually fly at great heights and therefore have few favourable opportunities for hunting. Moreover, the gliding and soaring is very energy-saving, and the most pronounced gliders therefore have only little need of nourishment during migration.

c) Birds of prey are sometimes seen to pursue a quarry but to break off the chase before catching up with the potential prey. There may also be only a slight attempt at pursuit: the bird suddenly changes its course and speeds towards the intended quarry but gives up after only a few metres of flight, resuming its original course. Predatory birds, especially sparrow-hawks, can also be observed to "start" when another bird passes close by; there is no pursuit but the short moment of "uncertainty" or "hesitation" indicates that the bird of prey was on the verge of giving way to another impulse. There are other instances when regular hunting takes place but the bird of prey slows down or turns away from the fleeing quarry before the latter comes within reach. I call this behaviour "incompleted attempts at hunting". As the predatory birds never actually tried to seize the quarry, these cases have not been included in the hunts reported below.

d) There remains now only those cases which should really be called hunting, viz., when a bird of prey makes one or more completed attempts to kill or seize a specially selected quarry. One hunt may consist of one or several stoops. If the first fails the birds often give up the hunt completely. Often, however, they continue the attempt, in many cases with amazing energy, striking repeatedly and violently, ten to twenty times or more, at the same quarry. After every unsuccessful stoop the raptorial bird is in an unfavourable position in relation to the prey and must therefore regain a good initial position before striking again. When calculating the percentage of successful hunts one might therefore be justified in considering each stoop, each new attack, as a hunt, that is to say, as a new number in the statistics. However, every new stoop in such a prolonged hunt is nearly always directed against the same individual, which has thus never eluded

the pursuer in spite of its efforts. If a predatory bird thus strikes many times in succession I have counted the whole course as only one hunt. If I have recorded, however, that the bird after one or more unsuccessful stoops began to pursue another quarry, this would be counted as two hunts. Such cases are rare, however, and are of no great consequence for the statistics.

e) It struck me very early how often the hunting of a predatory bird failed. For every successful hunt there are 10, 20, even 30 unsuccessful ones. During my earlier years of observations, I did not always note unsuccessful hunts which I witnessed, but all successful ones were naturally recorded. From 1942 this source of error has been greatly reduced. On certain days, however, when the flight of migratory birds has been very heavy, I have not had time to write down all unsuccessful hunts.

f) Finally, it should be pointed out that it is not always clear from the wording in my diaries whether a certain bird of prey has been actually hunting or only on the look-out for quarry. Such doubtful cases have not been included in the material submitted below.

What has been said on the previous pages, especially in section (e) and (f), shows on statistical treatment of the material the same tendency, i. e., that the percentage of successful hunts is too high. The first source of error can be eliminated if the percentage of successful hunts is calculated only on the observations from the years 1942 to 1947. It is naturally desirable, on the other hand, that all the successful hunts are taken into account in the discussion of the hunting methods of the various species of predatory birds. The treatment of the material, influence of the sources of error, etc., are discussed for each separate species.

No attempt has been made in this paper at a detailed mathematical analysis of the material. I am not in a position to judge whether anything essentially new can be obtained through such an analysis. Many factors in the hunting and selection of prey of predatory birds cannot be expressed in figures, however, and a purely biological treatment will therefore always play an important part.

Sparrow-hawk (*Accipiter nisus* (L.))

The sparrow-hawk is largely a short-distance hunter. It is rarely successful in catching a bird flying in open air and is often seen to pass close to migrating flocks of small birds without attempting to chase them. If, however, it should come very close to a small bird in flight, it is always ready to strike, accelerates with lightning swiftness, and displays remarkable skill in manoeuvring. Apparently it prefers to attack birds which are surprised when rising or in other situations when they lack their full freedom of movement.

Because of the situation of my observation stations I often observed the hunting of the sparrow-hawk in more or less open country. I suspected that my observations were not entirely representative with regard to this species since it is known to have a preference for hunting in woods and copses where it is less readily observed. The percentage of successful hunts might not be the same in woodland as in open country. My apprehensions seem to be unfounded, however. L. TINBERGEN (1946, p. 193—197) has found that the Dutch sparrow-hawks hunt in very varying terrain. During the breeding period they seem to avoid the open fields but "after fledging time their interest seems to be directed to the neighbouring fields as well ... The preference for woods only exists in early spring ..." The sparrow-hawk is undoubtedly very skilful at taking cover even on open ground. In Falsterbo where I have seen many thousands of sparrow-hawks pass they are often observed "to fly very low, on a combined hunting and migration flight. They approach with moderate speed, glide smoothly in among the bushes and dense saplings; they even follow the contours of every knoll and have an incredible ability to hide behind the smallest irregularity. They are always prepared to attack" (RUDEBECK, 1947, orig. Swedish). The sparrow-hawks migrating over Scania, the majority of which no doubt consist of Swedish and Finnish breeding birds, are observed to hunt in terrains of very different character. Although they come from very well-wooded countries they show no aversion to hunting in fields and meadows; on the contrary, they are often seen to attack various small birds resting on such ground.

Discussion of the observations

In my diaries I have records of 190 hunts by sparrow-hawks on non-predatory birds. I have been able to follow these hunts from beginning to end or at least sufficiently to study the hunting method and decide the final result. They gave a total of 23 victims altogether. (See table 1. The tables are placed at the end of the paper.) The fact that many unsuccessful hunts have not been annotated is especially true of the sparrow-hawk. The percentage of successful hunts is thus considerably lower than indicated by the table. This fact is further discussed below.

I have also recorded 23 hunts and completed attacks by sparrow-hawks against other predatory birds (table 2). None of these were successful. I have been in a quandary as to whether to include the attacks against other predatory birds in the hunting statistics or not. It is obvious that birds of prey are only rarely caught by the sparrow-hawk. It is not always easy to decide whether the attack of a predatory bird against large, "inadequate" animals has the character of real hunting or only of mobbing, undertaken

for other reasons. A sparrow-hawk that attacks such birds as kites (*Milvus*) or marsh-harriers (*Circus aeruginosus*) can hardly be successful! The same is probably the case with crows. I have hesitated to include such "hopeless" cases in the statistics. On the other hand, there is no doubt that a sparrow-hawk can kill smaller birds of prey, and it is not at all certain that the attacks of the sparrow-hawk against, for instance, kestrels and merlins should be excluded from the discussion. Many species of birds constitute the diet of the sparrow-hawk; some are taken in great numbers, some only to a small extent, and some only exceptionally. Many species are inconceivable as prey. The limits between these categories are, however, indistinct, and attacks may evidently occur also against inadequate objects. The latter must react in some way, however, either by flight or counter-attack, otherwise we get examples of atypical prey. For instance: wood-pigeons (*Columba palumbus*) are not usually attacked by sparrow-hawks — large migrating flocks often pass quite near the sparrow-hawks without being attacked. I have seen this phenomenon many hundreds of times since both species are very easily observed when migrating over Scania. Only once have I observed a sparrow-hawk forcibly attack a wood-pigeon in a small migrating flock. The pigeon reacted remarkably late; it veered aside at the very last moment, otherwise it probably would have been killed. Perhaps the same thing would happen if, for example, a kestrel did not dodge or defend itself in time? It is, on the whole, hardly possible to draw a distinct boundary-line between real hunts and attacks against inadequate objects. It should also be borne in mind that a specialization on rare prey or an aberrant mode of hunting is of fairly great interest from a theoretical point of view, whether a selective effect is found or not.

One type of hunting, however, has been consistently excluded from the statistics, viz., hunting or chasing of birds of the same species. It is not always possible for an observer to determine whether two sparrow-hawks which have a scuffle together in the air, are actually fighting or only "playing". According to LORENZ (l. c. p. 372—373), most predatory animals have inhibitions which prevent the killing of their own species. NIETHAMMER (1938) says, however, "je nach den Nahrungsbedingungen reguliert sich der Sperberbestand von selbst, notfalls durch Kannibalismus". I do not know on what NIETHAMMER bases his statement. Although LORENZ' theory is not always applicable I am of the opinion that the "attacks" made by the sparrow-hawks against each other, as a rule, do not have the character of real hunting and that the error would be increased if such cases were included in the statistics.

If the material is added up in conformity with the above principles one finds that 23 hunts of 213 gave results, i. e., 10.8 per cent. If hunting of

predatory birds are excluded the figures are 23 out of 190, i.e., 12.1 per cent. On account of the incompleteness of the diaries with regard to unsuccessful hunts before 1942, it would be more correct to calculate the percentage only on the material collected during the years 1942 to 1947. The figures will then be 20/203 and 20/180, respectively, i.e., 9.9 and 11.1 per cent.

There are several contributory factors, however, that make even these figures too high:

- a) Even during the years 1942 to 1947 many unsuccessful hunts were not recorded.
- b) All dubious cases are excluded from the hunting statistics.
- c) The definition of the concept of hunting as adopted here is a narrow one (cf. p. 74).
- d) Observations were chiefly made during the autumnal migration in Falsterbo, that is to say in a place where birds are abundant. This is true both for sparrow-hawk and suitable prey of various kinds. The percentage number of successful hunts is therefore probably comparatively large. On certain occasions this is definitely the case, see for instance October 13, 1942. Compare also DROST, 1930, for a similar case.

It should also be mentioned that my most comprehensive annotations and most detailed observations are from 1944, when I was in Falsterbo from August 1, to November 13. It appears from table 3 that the number of successful hunts that year was only about 5 per cent of the total amount. I am of the opinion that the hunting of the sparrow-hawk is successful in one case out of twenty, or perhaps still less frequently.

Of the 190 hunts on non-predatory birds, at least 163 consisted of attacks made from a short distance. 13 other cases which are noted down less carefully, can also be added to this group. The mode of hunting showed some variation, of course: some hunts were of very short duration, others could be characterized as eager pursuit, others consisted of repeated stoops against one and the same prey. The total number of completed attacks and attempts at seizure probably amounts to about 500. A total of 22 victims was taken during these hunts.

The remaining 14 hunts were all attacks from a great distance but varied in other respects. In a few cases the sparrow-hawk made an extremely rapid attack in an almost horizontal course towards the prey. A song-thrush, which was quite easily observed in a leafless hedge, was taken in this manner (case no. 9 below). I have seen a few other instances when sparrow-hawks used a hunting method similar to that employed by the peregrine falcon: a rapid and powerful stoop in a long, straight course, slanting down

towards birds in mid-air. However, all such attempts failed. In its extreme form this hunting method appears to be very rare.

Sometimes, especially during the migration seasons, sparrow-hawks may practise a peculiar mode of hunting, which seems to have been given little attention so far. Sparrow-hawks at a very great height, often 200—400 metres, suddenly plunge downwards in a very steep course. Sometimes, they dive almost vertically, other times at an angle of perhaps 65° to 75° , in a steep, but not always quite straight, course all the way to the ground. During the dive they fold their wings, the wing tips are directed backwards, the alulae are stretched strongly forwards and the legs downwards, preparatory to seizing the prey — a most remarkable sight. Obviously they are striking at a prey on the ground or very close to the ground.

I did not become more closely acquainted with this mode of hunting until late in the summer of 1945. Since then I have seen it used many times, almost exclusively by birds on migration. I have never observed them capture a quarry during these hunts; the final outcome is, however, often unknown to the observer. I am, therefore, not in a position to give any opinion as to the effectiveness of the method. The technique has, however, one disadvantage: Although the prospective victim is selected from afar and under circumstances which allow the bird to approach very rapidly because the prey is on the ground, the hawk must brake abruptly before reaching its quarry. The advantages of this technique are thereby largely eliminated, in contrast to the mode of hunting employed by the peregrine and the merlin.

Nevertheless, short-distance hunting is by far the most common hunting method of the sparrow-hawk. I agree, therefore, on the whole with TINBERGEN (1946, p. 97, 194) when he says: "Generally speaking, there seems to be little individual variation in the hunting technique."

Successful hunts of the sparrow-hawk

The following list includes my observations on the successful hunts of the sparrow-hawk, together with comments. Case 1 was observed in Hälsingborg, nos. 2 and 3 in the Krankesjö-area, previously well-known for its abundant birdlife, approximately 20 kilometers east of Lund. All the other hunts were observed in Falsterbo.

1. February, 1929, during a very cold and snowy winter. A great number of bramblings (*Fringilla montifringilla*), some greenfinches (*Chloris chloris*) and other finches as well as a blackbird (*Turdus merula*), which lacked several tail-feathers, were at a feeding-place for small birds outside my window. I had observed the blackbird at the same place for some time.

Suddenly a sparrow-hawk made a surprise attack and seized the blackbird, the only specimen present which to my knowledge was abnormal. It may, however,

have been taken not on account of its defectiveness but because it was easily noticed.

2. October 17, 1937. A female sparrow-hawk was flying quite low over a sandy stubble-field. Suddenly it wheeled around rapidly, alighted, and almost disappeared, although the ground was flat and the vegetation very low. Two starlings (*Sturnus vulgaris*) flew up where the hawk alighted. After some minutes the hawk arose again with a starling in its claws, but settled in a bush surrounded by tall grass. Frightened, the sparrow-hawk flew up from the ground near by without its quarry. The starling was soon found sitting in the grass. It had been plucked on a small portion of the upper back but was otherwise uninjured. There was no sign of blood on the bird, and the legs and wings were unbroken. When released, the starling uttered a faint "ürrrr" and flew off.

This was a surprise attack from a short distance. The sparrow-hawk was flying low but did not otherwise take cover. Apparently it discovered the starlings rather late — but before any one of the three birds noticed the danger. The flock of starlings, consisting of only three individuals, was remarkably small. The sparrow-hawk appeared probably at a moment when the three starlings happened to be in such a position that they did not observe the danger. Such a coincidence must be practically out of the question for large flocks of starlings.

3. December 19, 1937. A large flock of yellow-hammers (*Emberiza citrinella*) in a court-yard were suddenly alarmed and all the birds flew up into surrounding trees. Suddenly an old male sparrow-hawk appeared, flying low with a male yellow-hammer in its claws.

This is another example of a surprise attack from a short distance. Although the actual moment of seizure was not noticed the observation has been included since the manner of capture was evident from the circumstances.

4. August 15, 1942. 0630. Five sparrow-hawks were seen together over quite flat and treeless meadow-ground. One of them seized an indeterminable small bird, the other 4 hawks started on migration flight and disappeared over the sea.

Unfortunately my annotations of the case are scanty but apparently this was another example of short distance hunting. It is possible that the small bird was in a very difficult situation as five sparrow-hawks appeared at the same time, but this is by no means clear.

5. August 27, 1942. 0549. A sparrow-hawk pursued and seized a wheatear (*Oenanthe oenanthe*). The wheatear was surprised while rising but was not captured until
6 } after a rapid pursuit in swerves and zigzags.
7 } October 13, 1942. 1200—1300. Both sparrow-hawks and song-thrushes (*Turdus*
8 } *ericetorum philomelos*) were extremely common in Falsterbo. I witnessed many
hunts, approximatively 10, at least 3 of which were successful.

During the night of October 12—13, an unprecedented number of song-thrushes had arrived at Falsterbo on autumnal migration. Gardens, parks, and brushwood overflowed with song-thrushes. They did not keep together in definite flocks but were present everywhere. At the same time sparrow-hawks were extremely common. The total number of sparrow-hawks in Falsterbo during this afternoon was at least 400, perhaps as many as 600.

The observations made in Skanör and Falsterbo at noon on October 13, were extremely interesting. On several occasions I saw sparrow-hawks chasing song-thrushes; they attacked from short distance among the trees and pursued their prey with frenzy. I had a definite impression that on that day the number of

successful hunts was much greater than normally. This is quite natural too, for hunted or frightened song-thrushes that had just avoided one danger were often attacked by other sparrow-hawks which appeared unexpectedly. Many times, moreover, song-thrushes were attacked from several directions simultaneously. — Many remains of chaffinches, blackbirds, and song-thrushes which had been eaten were found in the brushwood. Most of them had quite obviously been caught by sparrow-hawks.

Never before or afterwards I have experienced such a great concentration of predatory birds and suitable prey in such a limited area. My colleague, K. G. WINGSTRAND, assistant at the Zoological Institute of Lund, had a similar experience in Falsterbo on September 30, 1946. The number of sparrow-hawks was enormous; the species of small birds dominating on that occasion were robins (*Erithacus rubecula*) and song-thrushes. WINGSTRAND on that evening saw great quantities of sparrow-hawks which "leapt in the bushes in pursuit of robins and song-thrushes". He considered the number of successful hunts to have been strikingly great on that day.

Cases like those described above are probably very rare, only occurring during migration periods and in localities where, for some reason or other, the migrating birds concentrate. They are thus special cases. But when they occur they are likely to cause a marked decimation of the number of prey present.

9. October 13, 1942. 1600. An adult male sparrow-hawk attacked a song-thrush which was sitting quite conspicuously in an open hedge. The sparrow-hawk came at a furious speed, simply seizing the song-thrush in the first attempt.

This was a surprise attack in an almost horizontal course of flight and from a comparatively great distance. — It should be noted that this observation was made on the same day as nos. 6, 7, and 8.

10. October 20, 1943. 0745. Two sparrow-hawks were flying along the coast-line in Falsterbo. They were "playing" with each other. Finally one of them disappeared; the other settled but rose soon again and started in pursuit of a goldcrest (*Regulus regulus*). The latter was finally seized in a swift turning movement less than one metre above the sandy shore. The sparrow-hawk alighted on a wrack bank with its prey.

During migration seasons, goldcrests are seen fairly often in such terrain, which actually is not at all suitable for them. Moreover, the behaviour of the goldcrest when faced with acute danger seems to differ considerably from that of other small birds. SVARDSON (1939) has aptly said, that panic is absolutely unknown in goldcrests. Panic in itself is of course no desirable quality, but a suitable, swift reaction of fear must be of the utmost importance, as far as one can judge. Many times I have observed goldcrests in exposed situations where they did not seem to show any such reactions. The percentage loss is therefore probably unusually high for migrating goldcrests.

11. October 25, 1943. 0705. A sparrow-hawk approached, flying low. Suddenly it was seen to pursue an indeterminable small bird which it seized in the air with an elegant sweeping movement.
12. October 27, 1943. 0955. A flock of approximately 200 starlings (*Sturnus vulgaris*) approached at a moderate altitude on migration flight. They were openly attacked by a sparrow-hawk. I did not believe it would be successful, as attacks on flying birds which can manoeuvre freely, rarely succeed. However, this sparrow-hawk was extraordinarily intensive in its pursuit, made several very powerful attacks and

finally dived straight down into the flock, seizing one starling. The sparrow-hawk, a fine old male, immediately settled with its prey. When frightened it moved only short distances at a time and seemed altogether unwilling to move. Perhaps it was exhausted from the chase?

I maintain that this manner of seizing a quarry is very unusual. Sparrow-hawks are often observed to attack freely flying birds but these hunts are practically always unsuccessful. The small birds attacked in this way do not react until the danger becomes imminent.

13. August 22, 1944. 0519. Two smaller flocks of starlings of 50 and 30 specimens, respectively, were seen over the open coast. They were simultaneously attacked by three sparrow-hawks. One of these seized a starling which happened to leave the flock. The starling was flying low, settling towards the ground when it was caught.

The wording of my annotations indicates that this starling left the flock without being particularly eagerly pursued. Then a sparrow-hawk at once attacked and seized the solitary bird. This would then be a striking example of atypical behaviour in a gregarious bird like the starling. In this particular case, however, several sparrow-hawks were pursuing the same flock simultaneously. When such instances occur, the position of the hunted animal is naturally much aggravated. It is doubtful, therefore, whether one is justified in this case in speaking of atypical behaviour on the part of the hunted starling.

14. September 14, 1944. 0620. A merlin (*Falco columbarius*) was chasing a young swallow (*Hirundo rustica*) flying quite low. The swallow made swift, long zig-zags in different directions, every time avoiding the falcon very gracefully. Suddenly a sparrow-hawk appeared at a tremendous speed flying only one or two feet above the ground, then rising a little it directly seized the swallow. The sparrow-hawk alighted with its prey. The age of the swallow was later determined from the remains of feathers.

The swallow could evidently manage the merlin but did not observe the sparrow-hawk until too late. Two predatory birds with different modes of hunting, which attack the same quarry simultaneously, naturally constitute a great danger. However, such cases are rare.

15. November 2, 1944. 1600. A sparrow-hawk pursued a small bird over ground covered with heather, bushes and small trees. The hunt was unsuccessful. The small bird alighted on the top of a small, thin birch where it was fully visible. The sparrow-hawk settled in the same tree, about 2 metres nearer the ground. When the sparrow-hawk rose, the small bird also took flight and passed over the sparrow-hawk. The latter made a rapid swerve and seized the bird.

This is a very curious incident, studied from close quarters. It is particularly remarkable that a small bird, which has been pursued by a sparrow-hawk and escaped, perched quite openly in the top of a small tree, all the more so as the terrain offered good protection. — The almost "impudent" manner in which the sparrow-hawk watched its prey is also curious. Finally, it is noteworthy that the small bird, which rose in fairly good time, should manoeuvre in such a way as to pass close above the sparrow-hawk!

Unfortunately I could not determine the species of the small bird, but it was probably a meadow-pipit (*Anthus pratensis*).

16. September 3, 1945. 0615. A sparrow-hawk flying extremely low over the open

grassy shore seized a bird in flight and alighted with it. From the remains of the feathers it could be established that the bird was a starling.

The hunt concerned one single bird. No flock of starlings is mentioned on this occasion. The species of the prey could not be determined while the hunt was in progress. I was surprised to find that it was a starling as solitary starlings are not common during migration periods. Such individuals are almost certainly defective in one way or other.

17. September 19, 1945. 0725. A merlin (*Falco columbarius*) was observed chasing a small bird over the grassy shore. The bird escaped, however, but a sparrow-hawk approached and seized it at the water's edge. Afterwards the sparrow-hawk flew away over the sea with its quarry, pursued by the merlin.

This is still another case of two predatory birds of different species attacking one and the same prey. As in the preceding instance (no. 14), the sparrow-hawk won.

18. September 27, 1945. 1455. While standing on "Ljungen", the heath near Falsterbo I observed with field-glasses a hen-harrier (*Circus cyaneus*) and a peregrine falcon (*Falco peregrinus*) tumbling together in the air. The ground in front of me was absolutely flat and there were no bushes for a distance of several hundred metres. Approximately 20 metres behind me there were some birch bushes, and behind these there was a vegetation of birch, willow, and bramble. — I stood still for a long time with the glasses before my eyes. Suddenly I felt a hard blow on the field-glasses which were pushed into my face. I turned around rapidly, catching sight of a sparrow-hawk diving into a birch bush. It reappeared immediately with a small bird in its claws, flew about 50 metres and settled in a thicket with its prey. After about 15 minutes I went there and found remains of the prey, a redstart (*Phoenicurus phoenicurus*).

This is an interesting and instructive case. Standing motionless there on the heath I was the only high object which could give cover to the sparrow-hawk. The hawk took advantage of this fact. It came from the large treeless region flying towards the birch bushes behind me. When doing so it took the only course which enabled it to approach unseen the bush in which the quarry was sitting. The sparrow-hawk thus flew straight towards me, passing so close over my head that it touched the field-glasses, dived into the bush behind me, and took the redstart by surprise.

19. October 1, 1945. 1025. A sparrow-hawk seized a freely flying song-thrush in a very swift attack at a comparatively great height — approximately 10 metres — over the flat grassy shore. The hawk alighted at once with its prey among some small pine bushes.

This case is quite remarkable. The song-thrush, as is known, is decidedly a night migrant and is rarely seen flying freely over the heaths, meadowlands, and shores in Falsterbo during day-time. When this does occur, it holds good only for isolated individuals which show evident signs of "migration restlessness", and the song-thrush in question behaved in this manner.

In addition it may be mentioned that the song-thrush avoids appearing in the open except during the singing period in spring. HORTLING (1929) has appropriately characterized its behaviour with the following anthropomorphic expression "The song-thrush lives in aristocratic seclusion and seems almost afraid to show himself". His words are especially true of populations in northern and eastern Europe. In western Europe, as is well known, the ecology of the species has changed and

the birds have become inhabitants of gardens and parks. This procedure has been going on in Scania for about 15 years.

20. October 16, 1945. 0740. A sparrow-hawk was pursuing a thrush over the sandy shore. The thrush was hard pressed but settled in a thick vegetation of *Atriplex* and became invisible. The sparrow-hawk alighted at the top of an *Atriplex* plant and remained motionless for several minutes. Finally the sparrow-hawk made a slight movement and the thrush took flight. (It should be pointed out, however, that it was impossible to determine with certainty which bird moved first. The thrush was in among the plants, invisible to me and probably also to the sparrow-hawk. It may thus be possible that the thrush moved first, whereupon the sparrow-hawk changed its position.) A new wild hunt followed quite close to the ground with rapid zig-zagging at very high speed. The distance between the birds was only a few centimeters. On one occasion the thrush lost some feathers but was not seized. The hunt continued and after a few metres more of intense pursuit the thrush was caught. The sparrow-hawk settled quite openly but in a shallow depression in the ground where it could not be seen. The hunt took place near to the observer. The prey was found to be a redwing (*Turdus musicus*). — I collected also the small feathers which were knocked off the thrush in the first, unsuccessful attack. These feathers were from the back of the bird.

This hunt was of uncommon intensity. Both birds evidenced a manoeuvring skill and a swiftness that were almost incredible.

21. October 27, 1945. 1435. A flock of exactly 15 chaffinches (*Fringilla coelebs*) on migration flight approached over the small dense pine grove near the light-house at Falsterbo. A sparrow-hawk made a swift attack and almost certainly seized one chaffinch. Fourteen specimens continued their migration.
22. October 31, 1945. 1130. A sparrow-hawk seized a chaffinch from a resting flock which was perched on telephone wires in a clearing in wooded terrain. This was a surprise attack from a short distance.
23. October 1, 1946. 0552. A sparrow-hawk seized a small bird, probably a goldcrest, while hunting over the open grassy shore. The small bird was flying low but rose slightly; the sparrow-hawk came in pursuit and caught the bird in a graceful ascending sweep. (This case was reported to me by K. G. Wingstrand.)

As pointed out above, my observations have chiefly been made in autumn. The successful hunts are distributed as follows:

February 1, August 3, September 4, October 13, November 1, December 1.

In two cases observed in October and in the December case I have expressly mentioned that the sparrow-hawk was an adult bird. Otherwise age and sex is usually not noted. I have noticed, however, when observing migrating birds, that only juvenile sparrow-hawks migrate in August and the first half of September; later, older birds also migrate but they do not become numerous and dominant until the middle of October. One can, therefore, be certain that the hunts prior to September 15 are performed solely by juvenile birds, the hunts after about October 15, on the other hand, largely by old birds. Regarding the interval from September 15 to October 15, it is difficult to express a definite opinion.

Discussion of the hunts

It is easy to recognize a sparrow-hawk in the field. It is often much more difficult to determine the species of small bird that is chased by a sparrow-

hawk, not because the small bird in itself is difficult to recognize but simply because many hunts take place at such a distance that the sparrow-hawk is still easily recognized but the small bird difficult or impossible to determine with certainty.

Another factor that complicates the determination of the hunted animal is the general hunting technique of the sparrow-hawk, for many attacks occur at very low altitudes, often more or less hidden by vegetation etc. Since even a determination of the species of the prey often proves comparatively difficult it is naturally almost impossible to notice abnormalities in them, such as discoloring, injuries, or such. A noteworthy or deviating behaviour is easier to discover if observational conditions are favourable and the normal behaviour of the various species are known.

Often the sparrow-hawk seizes its prey so rapidly that the latter hardly has time to react but is caught where it is, or when taking wing, or at least before gaining enough speed to manoeuvre freely. Examples are cases nos. 1, 2, 3, 4, 6, 7, 8, 9, 11, 18, 21, and 22. A few of the special cases mentioned below can also be assigned to this category. Sometimes, but not as often, the prey is seized after a prolonged chase (nos. 5, 10, 16, 20, and 23), which may be either in the form of an unbroken pursuit or divided more or less clearly into several stoops. In the latter case the sparrow-hawk seeks every time a favourable position of attack. This method, however, is far more distinctly and typically developed in the merlin and still more so in the peregrine.

The sparrow-hawk often attacks birds flying in mid-air but usually only from a short distance and when a surprise attack is possible. These hunts, however, almost always fail.

Some of my observations are probably not typical as they were made during migration periods in a place where very great numbers of predatory birds and prey were assembled. I have thus in two instances (nos. 14 and 17) seen a sparrow-hawk strike down a small bird which was already pursued by a merlin, and in another case (no. 13) three sparrow-hawks were observed to attack two smaller flocks of starling during which one of the hawks seized a bird. A comparatively great number of successful hunts occurred during the course of one day when an extreme concentration of sparrow-hawk and song-thrush occurred in the same place (nos. 6, 7, 8, and 9, discussed above).

Sparrow-hawks with untypical hunting methods have been observed in a few cases; no. 9 exemplifies a successful long stoop, no. 12 showed amazing swiftness, power, and tenacity in its attacks on a flock of starlings.

Only in one case (no. 1) was abnormal appearance, damage, illness, or anything of that kind noted in the prey. On account of the mode of hunting

such deficiencies must necessarily be difficult to observe even if they occur quite frequently. I observed, however, also some instances of deviating behaviour in the prey:

- No. 9 (song-thrush perched unusually openly)
- No. 10 (goldcrest in unusual environment)
- No. 13 (probably wrong behaviour in starling)
- No. 15 (extremely remarkable behaviour of pursued small bird)
- No. 16 (solitary starling)
- No. 19 (song-thrush which showed migration restlessness in the daytime and appeared in a very unusual environment)

Nos. 2 and 23 may perhaps also be included in this group.

I am quite aware that these observations alone cannot be made the basis of categorical statements. Certain cases are slightly ambiguous or may perhaps represent a special case (no. 10). On the other hand, it is obvious that the blackbird in no. 1 was defective and that nos. 9, 15, 16, and 19 displayed unusual behaviour. Consequently, in five cases out of 23 atypical qualities in the prey could be established. This is a high frequency, at least of an entirely different order of magnitude than that obtained when studying defects and abnormalities of birds in the field. It indicates that the sparrow-hawk seizes first of all those animals that are defective in some respect or show less suitable reactions, etc. This assumption is naturally borne out by the fact that the sparrow-hawk so often misses its quarry.

The attacks of sparrow-hawks against flocks of birds must be discussed separately. Such attacks are very common during migration periods and in the winter; at least 60 of the 190 hunts were directed at flocks, and prey was seized in 5 cases (nos. 3, 12, 13, 21, and 23). It was impossible to decide whether the hawk from the beginning concentrated upon any particular individual in the flock or if it attacked the flock as a whole, selecting its prey only when the result of the fright reaction became evident. Sometimes, however, it seized a bird before any individual in the flock had had time to react appreciably. It is difficult to believe in a selective effect in such cases, except in such instances when one individual differs from the others in colour, position, movements, or so on.

Predatory birds are sometimes seen with recently captured quarry although the hunt itself or the moment of seizure was not witnessed. I have recorded about 15 of these cases as far as the sparrow-hawk is concerned. In most of these instances it is, of course, impossible to draw any conclusions as to the condition of the killed animals. I experienced one interesting exception to this rule. In October, 1944, a solitary dunlin (*Calidris alpina*) was observed at the so-called Nabben, i.e., the most southwestern point in Falsterbo,

where the Sound and the Baltic Sea meet. In spite of the fact that several small flocks of dunlins passed and sometimes alighted for a while this bird never joined a flock but kept to itself all the time. This is particularly remarkable as the dunlin is a very social bird during migration. The behaviour of the dunlin was in other words entirely atypical and it was easy to see that it was not well; most of the time it stood still and was not at all as lively in its movements as a normal dunlin, but no external injury could be observed. On October 12, it was quite alone on Nabben the entire morning but was then seized by a sparrow-hawk. I did not see the actual hunt but arrived shortly afterwards when the sparrow-hawk was devouring its prey.

(Continued from *Oikos* vol. 2, 1950)

The Merlin (*Falco columbarius* L.)

Biotope and modes of hunting.

The merlin, *Falco columbarius*, is seen hunting only in open country. The hunting takes place at varying heights, often very low. The merlin generally stoops at flying prey, but it can also seize a quarry on the ground. The latter mode of hunting has been considered rare or accidental (see for instance TUCKER in WITHERBY et al., 1945), but DURANGO's observations (1948) indicate that it is used more often than has been assumed. According to ROSENBERG (in HOLMSTRÖM et al., 1944) the merlin seems even to be able to subsist on a diet composed mainly of lemmings (*Lemmus lemmus*), when they are abundant. —In spite of these exceptions, however, the hunting of flying prey is much the commonest, and my own observations concern almost entirely such cases.

The merlin can be characterized as assiduously active and always ready to hunt. It is often seen on migration flight, flying swiftly, low, and with a pronounced buoyancy in its movements, and then, perhaps, suddenly altering its course at a sharp angle with an increase of speed, but still very low. On such occasions it has noticed a small bird at a great distance and immediately engages in pursuit. Although the merlin does not seek cover in the same way as does the sparrow-hawk, it often succeeds in coming close to its prey without being observed, probably on account of its flying so low. At times the flying technique itself is probably a protection against discovery (see below).

If the first stoop fails the merlin often gives up the hunt at once, flying off at a high speed. Fairly often I have seen it chase several different small birds in rapid succession. If the selected prey observes the danger at an early stage so that the initial position of the merlin becomes unfavourable, it often does not continue the attempt but rushes after another quarry—often with just as little success. The merlin can, however, also be exceedingly persistent and

hunt one bird for a long time. On such occasions it displays a most surprising endurance in addition to great agility and swiftness in its movements. After an unsuccessful stoop it is a question of one second or another before the merlin is ready for a new attack. It can stoop twenty to thirty times in rapid succession. If the attacked bird does not manage to save itself in the vegetation it is forced upwards to ever greater heights. On repeated occasions the birds have risen so high that I have not been able to see the final result. In clear weather I have even seen a merlin pursue a swallow, rising so high that the swallow disappeared completely, even in the field-glasses: the tiny merlin was seen to stoop several times at its invisible prey at an enormous height. The falcon could be followed with the field-glasses only with great difficulty, and it was impossible for me to observe the result of the hunt.

In these cases the falcon thus uses an exhaustion technique, which, however, is unsuccessful in most cases. In the end the small bird generally plunges downwards in a long, steep dive. The falcon attacks again, and its last stoops will consequently be long, steep, and very violent, resembling those of the peregrine falcon. I have often had the impression that the small bird was completely exhausted and only swerved limply aside. The merlin, nevertheless, failed to seize its quarry, and the small bird finally fell down in the vegetation out of danger. In rare cases, however, this exhaustion technique succeeds, and it stands to reason that this occurs most often with prey in less vigorous condition.—

All hunts of the merlin do not develop in this dramatic manner. Often the birds remain very low, the falcon stoops again and again in rapid succession, attacking from short distances at a few metres up to approximately 20 to 50 metres. At times the falcon appears to be flying up and down like a shuttle while the quarry does not seem to make any headway. Also in such cases it may seem as if the prey becomes exhausted, but nevertheless the falcon fails in the great majority of cases.

The flight of the merlin is generally as described by TUCKER (l. c.): "buoyant, impetuous and dashing, with quick, winnowing wing-beats and occasional intervals of gliding." The flight often seems wild and vigorous although the bird is so small. The merlin possesses an extraordinary capacity to turn round and to make sudden zig-zags at great speed. It reacts with utmost swiftness and is full of vitality; it may almost seem to have a nervous vibration in its movements. The latter is sometimes so pronounced that one has the impression of an entirely new flying technique, and the bird takes on a changed appearance. The tips of the wings are directed backwards, the "wing knuckles" (i. e. the wrists) become still more pronounced and lie close to the sides of the body. The wings are thus not fully extended but are moved in a way similar to that of small passerine birds. The wing-beats become trembling and ex-

tremely rapid. Gliding on outspread wings is of course impossible in this position, but the wings can be kept still for short moments during which the bird glides ahead by its own momentum as many small birds do. The tail is narrowed and closed. Thus many factors contribute to give the merlin an appearance resembling that of a small passerine bird. It is perhaps most suggestive of a thrush (*Turdus*), but can also be compared to a lark (*Alaudidae*) or a swallow (*Hirundinidae*). Further notes on this behaviour, especially when used for hunting purposes, will follow below.

Discussion of the observations.

I have recorded a total of 155 hunts by merlins. If crows, magpies, kestrels, and sparrow-hawks are excluded as "inadequate" game, 139 hunts remain with 7 quarries in all. Thus 5 per cent of the hunts were successful. If the percentage is calculated only on the observations made during the period 1942 to 1947, which is most correct, the percentage of successful hunts is equal to 4.

As regards the representativeness of the material, it should be pointed out that also here all dubious cases have been omitted from the statistics. Other sources of error mentioned in the chapter on the sparrow-hawk (1950, p. 79), which resulted in too high a percentage of successful hunts, may also influence the results presented for the merlin though to a considerably lesser degree. In my opinion the merlin succeeds in striking down its prey on every thirtieth hunt at the most.

For the relative frequency of the various modes of hunting, see table 2. On account of the border-line cases it was sometimes rather difficult to tabulate the hunts; the majority of cases could, however, easily be classified.

The most common mode of hunting is a swift surprise attack, generally from a short distance without any attempt of seeking cover. The course of flight is, as a rule, approximately horizontal, but may also be directed obliquely downwards or upwards. Nearly all these hunts take place very low. When the attack fails the falcon very often ceases hunting, but sometimes the hunt is continued, developing into a short intense chase.

Prolonged persistent hunts are also fairly frequent. It is easily understood that the final results of prolonged hunts are often impossible to observe since they take place at a great height. For this reason quite a number of cases had to be excluded from the discussion. This mode of hunting is thus probably more common than appears from the figures submitted in this paper.

Only on three occasions have I seen the merlin start hunting by a violent stoop sloping downwards from a fairly great distance, rather like a peregrine falcon. These three hunts were unsuccessful. Finally, it should be mentioned that the attacks of the merlin on other birds of prey sometimes are in the form

of swift assaults and sometimes of persistent mobbing. The latter method is also used against crows and magpies, that is to say, against larger species which are not attacked normally. This may be a reason for not regarding them as actual hunts.

Successful hunts of the merlin.

The first observation reported below was made near the lake Krankesjön to the east of Lund. The other observations were all made in Falsterbo.

1. April 30, 1939. A merlin chased a sky-lark (*Alauda arvensis*) intensely for a very long time. The falcon stooped 30 to 40 times. The birds gradually rose very high. Finally, the lark plunged steeply downwards; the falcon stooped again, almost certainly seizing the lark in a long and very steep swoop. This is the only typical exhaustion hunt, witnessed by me, which did not end as an obvious failure.

2. September 8, 1942. 0635. A merlin, almost certainly a young female, was sitting on a wrack bed close to the shore. It rose, seized a white wagtail (*Motacilla alba*) and flew off over the sea in a south-southwesterly direction, undoubtedly on migration flight.—A good example of a short, swift hunt.

3. October 13, 1942. 1530. "A merlin was flying in hunting flight with half folded wings and very rapidly vibrating wing-beats. In flight it resembled both a swallow and a thrush. — It seemed as if its amazing similarity to a small bird were advantageous. It was flying very fast. At first it pursued flocks of sky-larks but failed; then it overtook another small bird, probably also a sky-lark, seizing it in flight without any difficulty at the first attempt. The hunt took place at a height of only a few metres over quite flat and open ground. The merlin attacked from a great distance but the prey did not seem to react at all to the presence of the predator. The falcon was an adult male. After the hunt it dropped to the level of the ground but continued for about a kilometer with the quarry in its claws."

4. October 6, 1943. 0928. A merlin approached over the flat seashore. It was flying extremely low and was hidden for a very short moment by a slight unevenness in the ground. When it appeared again it carried a quarry in its claws. It settled but was frightened and flew off with its quarry. Immediately afterwards a merlin with a prey in its claws passed on migration flight towards the southwest, almost certainly the same bird.

This was a typical surprise attack. The actual seizure was not observed, but the hunt was exceedingly short. When I noticed the bird it seemed to be on migration flight, not hunting a prey already observed. The quarry must have been seized at the very level of the ground, perhaps even on the ground. The merlin was out of sight only for about one second. I will not deny that

the bird may have had time to alight, but most probably it seized its quarry in flight without stopping.

Unfortunately, I could not determine the quarry as to species. Meadow pipit (*Anthus pratensis*) and siskin (*Carduelis spinus*) had been noted in the same place immediately before, and it was therefore probably one of these species. The bird seized was alone.

5. September 3, 1944. 0834. A merlin pursued a blue-headed wagtail (*Motacilla flava*) and seized it; then it immediately continued on migration flight out over the sea with the prey in its claws. A short and swift hunt!

6. October 10, 1944. 0702. A male merlin chased a small bird. The latter was seriously attacked, the falcon stooped and harassed with great intensity. The hunting took place very low over open ground, partly in wide swerves around some large bushes. The small bird did not settle in these bushes although it seemed to have a chance to do so on one or two occasions, but was finally seized. The falcon alighted at once with its quarry. Some 15 minutes later I walked to the place to determine the species by the plucked feathers. It was a chaffinch (*Fringilla coelebs*).

When I first discovered the merlin the hunt was already in full swing. I do not know, therefore, for how long the pursuit had been going on, but in any case it was a comparatively long and intense hunt. The behaviour of the chaffinch was very peculiar.

7. September 22, 1945. 0655. A merlin flew low over open ground near the shore, first frightening off a flock of linnets (*Carduelis cannabina*) and then a white wagtail. It did not chase them, however, but continued at full speed towards the southwest out over the sea. A small scattered flock of swallows (*Hirundo rustica*) was flying in the same direction; the merlin seized one of those at the first attempt, in a short, straight hunting flight ending in a tremendously rapid oblique swing upwards.

This is a typical example of a surprise attack, quite free and open, but so swift that the swallow did not seem to have time to react. During the final attack the merlin flew with swift vibrating wing-beats and half-folded wings, in a way strongly resembling the flight of a small passerine bird.

Thus, out of seven successful hunts three (nos. 2, 4, and 5) were rapid surprise attacks from a short distance. No. 3 was made from a greater distance and in typical "small bird flight", no. 7 was a very fast attack also from a greater distance. No. 1 was a very long exhaustion hunt and no. 6 a prolonged fierce hunt. Most quarries were undoubtedly taken by surprise attacks.

Discussion of the hunts.

Injury or illness was not observed in the birds captured. However, in most cases it is almost impossible to observe such things with certainty, owing to the swiftness with which the hunts are performed. Peculiar behaviour of the prey, on the other hand, was observed in at least one case, viz., in the chaffinch in hunt no. 6. Several times I have seen small birds escape a pursuing merlin by alighting in a bush or in high grass at the very last moment. On such occasions the merlin will usually interrupt the hunt and fly off, but sometimes it has been seen to stop for a moment as in consternation. In a few cases it even attempted to hover over the spot where its prey disappeared, but I have never seen it alight, not even in the vicinity. Thus it must be considered a very untypical behaviour on the part of the chaffinch that it did not settle, especially since the distance between the two birds at certain moments was not particularly short.—Otherwise the number of successful hunts of this species witnessed by me is too small to allow any far-reaching conclusions.

The merlin rather often attacks flocks of small birds. I have seen it at least 23 times, but none of these hunts was successful.

In addition to the report on hunt no. 3 a few words may be said about the merlin's curious habit of sometimes flying like a small passerine bird.—From my diary I quote the following lines:

September 18, 1942. 0855. "A merlin passes on migration flight high up in the air. In a quite remarkable way it resembled a swallow, in outline as well as in behaviour. Nearby and at a somewhat lower altitude there were several swallows (*Hirundo rustica*); they kept quiet and silent and apparently did not recognize the merlin as a source of danger."

GEYR VON SCHWEPPEBURG (1942), on two different occasions, noted a merlin flying in a very peculiar manner in the midst of a flock of swallows, which showed no fear at all. The falcon succeeded in seizing a prey: "... der Vogel flog langsam in dem flatterigen Schwalbenfluge dicht an eine der ohne allen Arg jagenden Schwalben, es war eine junge Rauchschatbe, heran und nahm sie ohne jeden Verfolgungsflug gewissermassen im Vorbeifliegen in die Fänge. Und dann änderte, dehnte und entfaltete sich plötzlich die bisher so klein und schwächig erscheinende Gestalt des Jägers: Er breitete schwebend Flügel und Schwanz weit aus, griff die schreiende Schwalbe anders, streckte die Fänge mit der Beute nach rückwärts und flog davon, — nun ganz deutlich und unverkennbar ein Merlin! — Bei den beschriebenen Beobachtungen konnte ich mich schwer des Eindrucks erwehren, dass der Falke sich, wenn auch unbewusst, in Schwalbengestalt tarnte, um Schwalben zu fangen. Das gelang ihm ja auch gut: er täuschte mich und viel besser noch die Vögel."

In all, I have witnessed 10 cases in which the merlin used this mode of flight

when hunting, but once only was it successful (no. 3 above). In some cases the pursued bird or flocks of birds, respectively, became frightened, in other cases the opposite was true. Of special interest are the cases when whole flocks of small birds were seen to be in close vicinity of a merlin without displaying any reaction of fear. Hence it must be concluded that this peculiar behaviour of the merlin is not included in ("einkalkuliert", LORENZ l. c.) the psychological make-up of the passerines. On the other hand, the observations evidence that even this method of hunting is generally unsuccessful.

Summing up, it seems probable that this interesting hunting behaviour would favour the seizing of prey without selective effect. Judging from the "normal" hunting methods and from the very high percentage of unsuccessful hunts, however, I am of the opinion that, on the whole, there is a selective effect.

The Peregrine Falcon (*Falco peregrinus* Tunst.)

Biotopes and Modes of Hunting.

The peregrine is in many respects the most interesting bird of prey for studying the modes of hunting and choice of prey. It hunts in open air, usually at a moderate or considerable height, providing good possibilities for the observer.

In spite of much persecution, the peregrine is still not rare as a passage-migrant in Scania. I have spent much time watching this magnificent bird and, in the course of years, gathered extensive field-notes on its hunting and behaviour. My diary for this species is rather accurate, consequently the sources of error, as discussed in the first part of this paper (1950, p. 79), are comparatively small, although not altogether absent.

The typical mode of hunting is by way of the famous stoop, the peregrine striking obliquely from above with an enormous speed at birds in flight. Very often the stoop is long and straight or almost straight, giving an overwhelming impression of strength, vigour, and swiftness. The stoop, however, is very variable in many respects. Sometimes the falcon will attack from a rather short distance, and there are all gradations between real stoops and mere mobbing. The stoop may be performed at a very flat angle or almost perpendicularly. I have seen a peregrine stooping at a small passerine bird for a distance of at least 500 metres at a rather flat angle before a wind of 18 metres/sec. The speed of course, was enormous. In fact, it was too high; the falcon could not perform its movements as precisely as necessary, and although the small bird was fighting its way slowly against the wind over the open sea, the falcon overshot its prey. — Steep or even perpendicular stoops are seen especially when the

prospective victim, after having been persecuted for a while, finally hurls itself to the ground.

Sometimes birds are pursued violently in a horizontal direction, or the falcon may try to catch a bird en passant, even quite low over the ground.

The perseverance of the peregrine varies much. Very often it will stoop only once, irrespective of the result, but now and then it will make another attempt or even go on stooping five or ten times, and in rare cases it will repeat its attempts 50 times or even more. When stooping several times in succession the peregrine always tries to force its victim to ever greater heights, simultaneously trying to get a favourable position for the next stoop.

Not uncommonly the peregrine is seen to whirl about with other birds in the air, sometimes in a seemingly playful manner. Such cases may, however, be serious enough, as can be seen from hunts no. 1 and 7 in the list below.

I have seen the peregrine hunt 260 times. If *Haliaeetus*, *Buteo*, and *Pernis* are considered "inadequate" prey and for that reason excluded from the statistics, the number of hunts is 252. Out of these, only 19 were successful, giving a percentage of 7.5. Thus the hunts are usually unsuccessful. This fact should be stressed, because the literature very often gives one the impression that the peregrine can catch its prey quite at will or at least very easily. This erroneous view is probably founded on old concepts of the peregrine as something quite perfect—and a perfect creature obviously cannot fail. TILLISCH, who recently (1949) published a very interesting book on the falconry, has (in litt.) informed me, that the tame falcons did not miss their prey nearly as often as indicated by my figures given above. According to TILLISCH, however, this is due to the fact that tame falcons are not cast off unless the falconer considered the chances favourable for a successful hunt. Thus the results obtained in falconry cannot be used in the same manner as those concerning wild birds.

Nevertheless, the peregrine is undoubtedly a very efficient bird of prey. Its usual mode of hunting claims great exactitude and ability, the more so as the peregrine usually does not rely on surprise but very often stoops at—and sometimes catches—birds which have observed the danger in due time. Besides, the bird sometimes may get its prey although the precision in stooping is not very pronounced—see, e. g., hunts no. 18 and 19. — For further particulars of the hunts, see table 3. In that table I have also included a number of hunts on the bat *Nyctalus noctula*, witnessed by me on October 25, 1937. These hunts were performed in the early afternoon in full sunshine.

Successful hunts of the Peregrine Falcon.

Cases nos. 1 and 3 were observed near the lake Krankesjön, no. 2 in the Karup meadows, a very good place for waders in the interior of Scania, no. 16

in Karlshamn in Blekinge, and nos. 17, 18, and 19 near Ottenby on the southern point of Öland. The remaining 12 observations were all made in the vicinity of Falsterbo in southwestern Scania.

1. March, 29, 1935. 1730, Several lapwings (*Vanellus vanellus*) were flying screeching around me. Suddenly a peregrine falcon appeared and started chasing one of the lapwings. The falcon stooped several times fairly swiftly and gracefully, but all the time quite low with short, moderately steep lines of attack. The lapwing skilfully avoided the predator by zig-zagging rapidly. I saw it several times swerve downwards so that the falcon missed and instead passed immediately above the intended prey.

After stooping in vain the falcon rose again, made a more or less marked "looping" and attacked once more. The hunting technique was the same throughout. Finally, the falcon hit the lapwing which sank to the ground with a scream. The falcon shot past but returned, settling on its victim. The stoop took place very low, the lapwing being struck only about one metre above the ground. The entire hunt was observed at very close quarters. Although I was standing quite openly on the meadow, the birds were sometimes only 10 metres away.

The falcon did not pluck the bird but sat still looking in my direction. Probably at this point it was frightened by my presence. It rose with its quarry but dropped it almost at once. The falcon alighted near by, screaming excitedly "kêack kêack . . .".

I picked up the lapwing. It could run but was unable to fly. There was a deep wound, as if made by a razor, in the breast muscles on the left side of the carina. In addition, the primaries nos. 6 to 10 in the left wing were cut off in a very curious manner, viz., at a very slight angle to the quills.

In spite of the fact that the stoop of the falcon was not violent I could not see how the injury was brought about. The nature and site of the injuries, however, made it very probable that the falcon hit the quarry with its hind claw. (Since writing this I have found that the falconers of former times generally were of the opinion that the falcon killed its prey with the hind claws (TILLISCH 1949)).

The mode of hunting of the falcon was interesting. As mentioned, the stoops were short and not violent. The total number of stoops were not noted but were probably about 15. The hunt had a touch of playfulness and resembled clearly those plays in which the peregrine is sometimes seen to engage with sparrow-hawks, crows, and other birds.

I had the lapwing stuffed. It was a female containing a walnut-sized egg.

2. May 11, 1936. 2030. In the evening when dusk had fallen waders and ducks were lively and flying around over the meadows. A flock of ruffs and reeves (*Philomachus pugnax*) was seen with several males in different plumage.

Suddenly a peregrine falcon appeared, most likely a female, and started chasing the flock. After several powerful but unsuccessful stoops the falcon struck a white-collared ruff. The blow was extremely violent. The ruff was flying almost horizontally at 20 metres' height at most above the ground. The falcon flew in the same direction but very much higher, rose still more, and then dived down obliquely towards the quarry at a tremendous speed. In the middle of the stoop the falcon suddenly changed its course, shooting vertically, or almost vertically, downwards with still greater speed. The ruff was hit from above, fell down on an inundation and lay there lifeless but plainly visible. Since the stoop occurred so low but at approximately right angles to the ground the falcon had to "level off", literally a fraction of a second after striking the prey. The falcon rose steeply, returned at once and circled for a long time above the dead ruff. It did not pick it up, however, but finally flew off.

The attack took place unusually late in the day. Perhaps a ruff with a white collar was killed on account of the feeble light; it must have been the most conspicuous among the birds.

3. August 7, 1936. 1845. A peregrine falcon stooped violently at a flock of about 4,000 starlings (*Sturnus vulgaris*) which arrived at the lake Krankesjön to spend the night. The flock closed in very compactly, with sudden swerves in various directions, so that the falcon was unsuccessful. Shortly afterwards another flock of about 3,000 birds approached. When the falcon appeared the flock plunged downwards in a body. The falcon made a powerful stoop, nevertheless, obliquely down through the flock and emerged with a starling in its claws. This occurred at the moment when the flock plunged rapidly downwards. After the completed attack the falcon was, therefore, close to the ground. It flew off with its prey. The starlings were extremely agitated and zig-zagged continually. When they passed over a stretch of open water, a loud splash was heard—it was the excrements of the birds falling into the water like a shower of rain.

4. September 30, 1941. 0750. A large flock of wood-pigeons (*Columba palumbus*) passed over Falsterbo on migration. A few minutes later the flock returned in close formation. When I was noticing this, two birds were seen to collide violently, not in the periphery but in the middle of the flock. It was a peregrine that had seized a pigeon in the right wing. The falcon started plucking at the neck of the pigeon with sharp rhythmic pecks. Every time a little down was torn off; it looked like a small cloud of smoke which appeared white in the sun and was dispersed by the faint wind. The falcon settled but was frightened, deserted its quarry and flew off, crying "kikikikiki".

The right wing of the pigeon was found to be broken. The fracture was on the hand between the sixth and seventh hand quills. The neck was torn open,

the trachea bared, and many feathers had been pulled off the neck, on the back of the neck as well as on the craw.

I did not see the beginning of the hunt. As in the preceding example the falcon stooped at a bird in the middle of a flock, not at an isolated specimen.

5. September 4, 1942. 0810. Some blue-headed wagtails (*Motacilla flava*) were observed on migration over the sea at a height of only a few metres. A peregrine falcon appeared from behind at a furious rate, started in pursuit of a wagtail and seized it after a few rapid swerves. The falcon then headed for land again.

6. September 14, 1942. 0550. A peregrine falcon was observed circling over the sea together with 8 sparrow-hawks. The birds did not stoop at one another but kept together in a distinct flock, a phenomenon very often observed during the autumn migration of birds of prey.—A flock of approximately 400 starlings started on migration flight in the direction of the predatory birds but lower down. Naturally the falcon stooped. The first attacks failed but one starling was forced to leave the flock. By means of skilful manoeuvring the isolated starling was forced higher and higher. When it finally made an attempt to plunge, the falcon made a splendid stoop, striking the quarry which fell into the sea from a great height. The falcon went down in a steep spiral, seized the starling, flew to the shore and started eating at once. Having finished its meal the falcon flew towards the southwest, tried an attack far out over the sea on a small bird of an undeterminable species, but failed, and continued its flight.

The behaviour of the starlings was remarkable—they flew directly towards a peregrine falcon which was soaring in front of them. The sparrow-hawks certainly had no frightening effect on the starlings since they rarely attack freely flying birds. The latter, therefore, do not react to sparrow-hawks until the danger is acute. It is well-known, however, that their reaction to the peregrine falcon is quite different, manifesting itself in violent alarm even if the falcon is not actually hunting. It is particularly remarkable that all the starlings in a large flock showed no attention. Perhaps the falcon escaped notice just while it circled together with so many sparrow-hawks? The question suggests itself whether all individuals of one and the same flock of starlings give any attention to what happens around them.—I did not notice any unusual behaviour on the part of the isolated and stricken starling.

7. October 1, 1942. 0705. A young male peregrine falcon was "playing" with two sparrow-hawks over the sea. The falcon stooped at them several times at a low height. The attacks were made from a short distance and without great precision or swiftness; the behaviour of the falcon was altogether markedly "playful". The sparrow-hawks displayed very little fear. Suddenly a strange thing happened: the falcon stooped as before but seized one sparrow-hawk in the breast, gashed the quarry in the neck once or twice and flew to the shore

where it settled with its prey. Another sparrow-hawk, probably the other of the two previously hunted, followed, apparently interested, and alighted in the vicinity without any attempt of worrying the falcon. The latter started eating. Some time later when the meal was still in progress, I approached the falcon. Several sparrow-hawks were sitting on the shore close to the falcon watching while it fed.

This peregrine specialized on sparrow-hawks. The day before when there had been a dense fog, I observed a male peregrine flying by with a screaming sparrow-hawk in its claws. Although I had not witnessed the hunting it is evident, on account of the weather, that the prey had been taken at close quarters. During this period I saw, moreover, a male peregrine falcon chasing sparrow-hawks on several occasions, and on October 2nd I came upon a falcon when it was eating a female sparrow-hawk in a street in Falsterbo! It cannot be doubted, that one male peregrine had killed three sparrow-hawks in three days. Probably this peregrine secured its prey rather easily. And this, in turn, might have been because the falcon specialized on a type of prey which did not constitute the normal diet of the peregrine falcon and which, therefore, reacted only insufficiently to the falcon as a source of danger. The mode of hunting was not typical but demanded much less energy than the typical method: the falcon made no surprise attack and no actual stoop; it simply took the sparrow-hawks when tumbling with them in the air.

It should, however, be pointed out that peregrine falcons are often observed to stoop more or less "playfully" at sparrow-hawks or other small predatory birds, but that these are very rarely caught (cf. UTTENDÖRFER 1939). My impression is that the sparrow-hawks, like other birds of prey, show comparatively little timidity of the peregrine falcon but that they are nevertheless on their guard. It is only natural that those individuals that expose themselves most carelessly will be most easily caught.

8. October 24, 1943. 0922. A flock of 35 wood-pigeons started on migration flight out at sea. A peregrine falcon followed at great speed and seized a pigeon. The whole event took place so rapidly that the flock did not have time to react. This observation was reported to me by K. G. WINGSTRAND, who acted as an observer in Falsterbo on that day.

9. August 23, 1944. 0550. A flock of 20 starlings flew out over the sea and was attacked by a peregrine falcon. One starling was forced out of the flock; the falcon stooped at it three times but missed. The starling succeeded in reaching the water level and flew towards the shore. It seemed for a moment as if the falcon had given up, it slowed down and made a swerve so that the starling got a good head start. Unexpectedly, the falcon changed its course, made another attempt and seized the starling close above the water. The falcon flew off with its prey towards the southwest, disappearing over the sea apparently on migration flight.

This case is interesting. At the very moment when the danger seemed to have passed the falcon attacked again—successfully. Perhaps this was due to the fact that the starling “relaxed” after having previously mobilized all its strength.

10. October 4, 1944. 0730. A peregrine falcon passed on migration flight after having unsuccessfully hunted a starling. At 0735 a small flock of wood-pigeons and stock-doves passed, also on migration flight. The falcon then returned, stooped at a pigeon in the flock and seized it in a swift attack. After having plucked the quarry, the falcon flew off over the sea but alighted with its prey on a small sandy island about 2 kilometres away.

11. October 5, 1944. 0645. A flock of approximately 40 wood-pigeons and 8 stockdoves flew out over the sea but turned back on account of a peregrine falcon that stooped successfully at a pigeon and then alighted with its prey on the shore. (The course of the hunt was not recorded in detail, but the falcon undoubtedly made a rapid stoop and succeeded in the first attempt).—Another peregrine falcon hunted a pigeon but failed and later made prolonged but futile attacks on the falcon which sat on the shore with its quarry.

12. October 20, 1944. 0900. Five wood-pigeons flew on migration flight out over the sea at a moderate height. A peregrine falcon came from behind in a horizontal course at an enormous speed, seized a pigeon, killed it in the air and continued to a little sandy island c. 2 kilometres distant. It was evident that the falcon had a bad grip of its prey, probably only in one wing. Over the sea the falcon was pursued by a large gull, probably *Larus argentatus*, and dropped its prey. Both the falcon and the gull circled around over the pigeon floating on the water but did not pick it up. The falcon soon continued towards the southwest and disappeared.

In this case the mode of hunting was unusually apparent: a remarkably swift attack directly from behind. The falcon probably approached the pigeon in the blind sector. It was evident that the pigeon did not react at all until the falcon was very close, approximately 20 to 25 metres. This distance the falcon covered in accelerated horizontal flight certainly in about half a second.

13. September 8, 1945. 1155. A peregrine falcon flew westwards over flat and open ground at a height of about 15 metres. Suddenly it changed its course at right angles towards the south, dropped almost to the ground and increased its speed. In this manner it flew about 400 metres, all the time very low. The falcon evidently had a particular quarry in sight. Just before observing the peregrine I had observed another smaller falcon alighting on a fence pole some 300 metres to the south. The peregrine made a horizontal attack, the little falcon flew up but was seized from below. The peregrine then settled with its quarry on the heath. An examination showed that the prey was an adult male kestrel (*Falco tinnunculus*).

This hunt is interesting from several points of view. The peregrine discovered its prey at a distance of approximately 600–700 metres with the light against it and immediately began the pursuit. Possibly, the kestrel was flying when discovered, but however that may be, the peregrine attacked it when sitting on a pole. The transition from migration flight to hunting flight was unusually apparent. Evidently, the kestrel did not notice the danger until very late but managed to rise with the result that it was seized oblique from below. Finally, the choice of prey was very unusual, although similar cases are known to have occurred (ENGELMANN 1928, NIETHAMMER l. c., WITHERBY l. c.).

14. October 11, 1945. 1220. Some 80 crows (*Corvus corone cornix*) passed on migration flight fairly high up, as usual in scattered and irregular formations with an average distance of 20 to 30 metres between the birds. A peregrine falcon appeared directly from behind at a great speed, flying horizontally, and seized one of the last crows in the flock. The falcon alighted with its prey. As far as I could see the crow did not have time to react at all. The falcon was undoubtedly flying in the blind sector of the crow, otherwise it must inevitably have been discovered, since it was approaching quite openly and from a great distance. It is evident that the last birds in a scattered group are the most threatened when the predatory bird uses this mode of hunting.

15. September 4, 1946, 1145. Different kinds of waders, mostly *Tringa* spp. and *Philomachus* were flying to and fro over the Fotevik, a very good resting place for migrating waders. A peregrine falcon began to pursue a single bird, almost certainly a wood sandpiper (*Tringa glareola*). The hunt started low down, but the birds rose continually, and finally they were at 500 metres' height at least. The falcon stooped again and again, steeply and powerfully, but the distance of attack of each separate stoop was not particularly long. The total number of stoops was not counted but must have been at least 20. The hunting went on for a longer time than usual. The technique was also remarkably good: the sandpiper was forced to rise practically incessantly. Towards the end of the pursuit the sandpiper made a few attempts to plunge downwards but was hindered by the falcon. Finally, at a dizzying height, the falcon succeeded in seizing the quarry in one precipitous stoop. After that it went down towards the ground and settled in an open place as is the habit of the peregrine falcon. — In this case there can hardly be any doubt that the falcon exhausted its prey, a mode of hunting that is fairly often used but generally fails.

16. September 25, 1947. 1125. A large peregrine falcon, which a few minutes before had been observed chasing a flock of pigeons, attacked the next flock, consisting of 350 wood-pigeons, seizing a pigeon in a magnificent precipitous stoop. The falcon settled with the quarry on a small rocky islet in the sea.

The whole attack was very sudden, and it was impossible to study the behaviour of the birds in detail.

17. October 17, 1947. 1100. A peregrine falcon and a great black-backed gull (*Larus marinus*) pursued together a pigeon whose plumage was rugged and torn. The pigeon was evidently not well, settled twice on the water and was very hard pressed. It was finally seized by one of its pursuers but I could not determine which one.

A good example of hunting inferior prey.

18. October 22, 1947. A young female peregrine falcon stooped at a flock of 21 stock-doves (*Columba oenas*). A few birds were driven out of the flock, and the falcon started hunting one of these with great frenzy. The pigeon escaped, however, and settled on the ground. The greater part of the flock of course had disappeared by this time. Another of the few isolated individuals did not, however, join the flock but was flying about quite openly at a height of about 150 metres. The falcon discovered this pigeon, started chasing it and stooped three times with a peculiar but apparently effective technique. The stoops were extremely powerful, long, and steep but badly directed. The falcon did not even seem to aim at the prey but struck in its vicinity and when it had passed the pigeon it swerved in an arc up towards it but, once more, without great precision.

The pigeon very soon got tired. After three stoops, all of which were gross failures, it was completely exhausted. I saw it fly quite close to the ground and disappear behind a low bush. The falcon followed, disappearing at the same point. I immediately went up to the place; the distance was approximately 700 metres. At the place where the pigeon had disappeared I found a little down and a drop of blood in the grass. The falcon had moved about 150 metres farther away and was plucking its quarry. The pigeon had reached the ground without being hit but so exhausted that the falcon could settle on it without difficulty.

This is a good example of an abnormal behaviour in the hunted animal. Instead of flying off while the falcon was engaged in the first hunt this pigeon remained in the neighbourhood, which was the sole reason for its being pursued and seized. The rapid exhaustion indicates that the pigeon was inferior also physically.

19. October 25, 1947. 0810. A flock of 110 jackdaws (*Corvus monedula*) approached at a great height. A peregrine falcon came from below and forced them still higher up, to about 700 metres' height. From the very beginning a few of the jackdaws lost contact with the flock; several "fell off" but were not hunted. When the falcon had almost reached the flock, some more fell off, and one of these was selected as prey. The falcon stooped many times with great strength but missed each time, sometimes grossly, sometimes closely. The jack-

daw reached the ground without being hit but was quite exhausted and alighted or, rather, fell down on the meadow. The falcon settled on it. The mode of hunting was the same as in case no. 18; the falcon was probably also the same. It is remarkable that the falcon did not attack any of the jackdaws that first left the flock. Whether the falcon from the start had selected a particular bird or whether it began the hunt when it reached a particularly favourable position in relation to one of the falling specimens could not be determined in this case: the first alternative seems to be the more probable.

Discussion of the hunts.

Before treating my own observations, a few words may be interpolated on the literature on the hunting methods of the peregrine, especially as far as the selective effect is concerned. ENGELMANN (1928) discusses the modes of hunting at length and concludes that the peregrine "hält Auslese und begünstigt so die Zuchtwahl. Die dümmsten, trügsten und schwächlichsten Stücke fallen ihm durchschnittlich doch am ehesten zum Opfer". I believe he is right to a rather great extent, but I have been unable to find, in ENGELMANN'S own account, any reason for this conclusion. He just gives a lot of information as to the swiftness, ability, and general behaviour of the falcon, but nothing else. BENT (1938), too, quotes many interesting observations; he does not enter into discussions on the selective effect, but many quotations give the impression that the peregrine can catch its prey almost at will.—Finally, part of the discussion in TILLISCH (1949; orig. Danish) may be quoted, as it gives an impression of the different views on the subject: "It is maintained, nay, it is almost a dogma, that birds of prey preferably catch weak and sick specimens. This is possible, yet the distinguished falconer JAMES EDMUND HARTING emphasizes that this is not true as far as the peregrine is concerned. HARTING also states that his view is shared by many falconers. . . According to HARTING, the peregrine will catch the strongest specimen out of a flock just as easily as the weakest one, and it preferably chases the bird which is first observed, a method used also by man.—On the other hand, there is of course much evidence in favour of the current opinion too. Thus. . . in one case it was found that all the partridges caught by (tame) peregrines were recently wounded by shooting."—I have not got the impression that the "dogma" mentioned by TILLISCH is generally accepted; it is true that the above view is fairly often met with, but I have generally met with a much more sceptical attitude, certainly on account of the scarcity of exact information.—

* * *

I have seen the peregrine perform successful hunts on 19 occasions. Out of the birds captured, no. 17 was a sick or injured specimen, and no. 18 displayed a decidedly abnormal behaviour. The sparrow-hawk, no. 7, was un-

usually tame and unwary. Probably, also hunt no. 19 concerned an inferior specimen. The flock of starlings mentioned in no. 6 definitely showed an abnormal behaviour, but as all the birds behaved in this peculiar manner the case cannot be quoted as a capture of an abnormal bird, even if the observation may be of interest as far as the psychology of social birds is concerned. Anyway, in at least three cases out of 19, i. e. in 16 percent, the bird captured was in some respect abnormal. Taking into consideration the difficulty of discovering abnormalities in the pursued birds, I think this percentage is high, especially if put in relation to the corresponding percentage generally seen in birds in the field.

In all I have seen the peregrine attack injured or obviously abnormal birds in six cases, three of which resulted in successful hunts, viz., no. 7, 17, and 18 in the list above. The other cases were as follows: a *Corvus corone corone* in a flock of *Corvus corone cornix*, a *Corvus corone cornix* without tail feathers, and, in a flock of *Columba palumbus* one specimen with very ragged and torn wings. Thus, within this category, the falcon was successful in 50 percent of the cases, while in the remaining 246 cases the corresponding percentage was only 6.5.

There is some evidence that the peregrine is especially attracted by birds which seem strange in one respect or another, not abnormal or injured specimens but, e. g., birds staying in an unusual environment (THIENEMANN 1931) or birds with conspicuous colours in relation to other species, such as Roller, *Coracias garrulus* (TISCHLER 1941) or Oriole, *Oriolus oriolus* (RAMEL, personal information). This corroborates my view that also birds with deficiencies of some kind are preferably attacked by the peregrine. Moreover, it seems to have interesting bearings on the influence of the peregrine upon rare birds, irregular vagrants, and so on.

The peregrine very often attacks flocks of birds. Among the 260 hunts observed, at least 100 were directed against dense flocks, and out of these 7 were successful. It is, however, not possible to draw a clear-cut line between the attacks on flocks and other hunts, because an attacked flock will often scatter and the subsequent hunt will concern one particular specimen, which was forced out of the flock. In such cases it is usually not possible to decide whether the falcon attacked just in order to get at one particular specimen, and, if so, whether that or some other one was forced out of the flock.

Summing up, it can be said that the modes of hunting in *Falco peregrinus* are much varied (cf. Table 3). Most often the falcon stoops at its prey, but the stoop can be performed in many ways, and the falcon may adopt other methods as well. Even a virtually playful mobbing may evolve into a successful hunt. The peregrine is an able hunter indeed, but from the reasons given above I conclude that it exercises a selective effect on the bird population from which it secures its prey.

The Sea-Eagle, *Haliaeetus albicilla* (L)

The sea-eagle represents quite another type of predatory birds than the preceding ones. It is large and rather heavy and not nearly so agile on the wing as are hawks and falcons although it may sometimes show remarkable swiftness. Only rarely can it secure its prey by surprise.

The sea-eagle is regular but nowadays rare as a passage-migrant and on hibernation in Scania. In winter it is most easily seen at several lakes in the southern part of the province. When the lakes are frozen, it is often seen sitting on the ice. The bird is in some degree social, two or three or even more specimens frequently being seen in company.

Most water-birds, except the swans, rise and fly off when they observe an approaching sea-eagle. However, if the eagle does not attack, they get calm almost immediately, and on the whole they react surprisingly little before a sea-eagle except when hunting or approaching. If the eagle is hunting over a large flock of ducks, often only those birds get frightened which are quite close to the eagle, the others do not rise until they are immediately threatened, as observed and described already by SWANBERG in 1931.

Table 4 gives a summary of the modes of hunting and the percentage number of successful hunts for the sea-eagle. Usually the eagle will fly at no great height over a flock of water-fowl, repeatedly attacking it and trying to snatch a bird out of the flock. The birds, of course, get frightened, but if they are too close to the eagle, they cannot simply rise and fly away, since just when starting they must keep a straight course for a relatively long distance, and when doing so they are rather easily caught. Thus instead of rising they often dive or just rush very fast along the water.

A hunt of this kind may go on for a long while. Sometimes the eagle will attack the same specimen several times in succession, but should another specimen come in a position more favourable for the eagle, this one will be attacked instead of the other. Often the eagle is seen flying over bird flocks, which rush wildly over the water in different directions. A considerable time may elapse between the really completed attacks, quite simply because the pursued birds manage to get away in time. Often the flocks of waterfowl will observe the danger so early that there will be no real hunt. At the southern point of the isle of Öland, where very large flocks of ducks gather in the autumns, I saw this mode of hunting or attempts at hunting almost daily for a whole month. Sometimes five sea-eagles were seen together. Nevertheless there were several days when the eagles, strictly speaking, did not hunt at all; they kept flying for hours over the ducks, making parts of the flocks go on the wing little by little, but they never attacked, because the ducks always observed the danger in due time. As there are obviously doubtful and debatable cases,

it is not so easy to define the concept of hunting and to distinguish between the separate hunts of the sea-eagle as in the other species discussed here. In Table 4, however, I have taken care not to put the number of completed hunts too high, and all doubtful cases have been omitted.

Deviating modes of hunting are sometimes seen. Thus, a few times I have observed the sea-eagle trying to catch grazing geese (*Anser fabalis*). The eagle was flying low over a flock of about 750 geese, which, of course, got frightened and dispersed into smaller flocks and flew away in different directions. It should be mentioned that many flocks alighted only 200–300 metres away and did not rise again until the eagle came very near. The eagle attacked flying or rising geese several times but always without success.

When the eagle is chasing other birds in flight, it sometimes shows amazing perseverance and agility. However, I have never seen it catch a prey under these conditions, but once a badly harassed *Larus argentatus* disgorged a piece of food, which was caught by the eagle in the air.

Twice I have observed the sea-eagle making very long and steep stoops against a flock of ducks on the water and a large flock of grazing geese, respectively, the latter attack being particularly violent and starting from a height of at least 600 metres. The geese observed the danger very late but managed to get away just in time.

A presumably rare case of an eagle hitting down a flying mallard is discussed below.

Successful hunts of the Sea-Eagle.

1. 1937, Nov. 18. The lake Krankesjön was partially frozen. In an open stretch of water there was a flock of about 300 mallards (*Anas platyrhynchos*), and on the ice rather close there were two young sea-eagles. One of the eagles rose into the air and flew towards the ducks, all of which took flight and rose into the air very densely packed "like a wall". The eagle was approaching quite low over the ice and was for a moment hidden by the rising ducks. At that very moment one mallard whirled out of the pack almost horizontally, fell down and slid along the ice at least 10 or 15 metres. It is perfectly clear that the eagle had hit the duck in passing in the flight, although it was not possible to decide exactly how the hunt was performed. The eagle passed over the duck, which was lying motionless on the ice, seized it without stopping and flew off, followed by the other eagle, which had taken no part at all in the hunt. A hooded crow appeared and attacked the eagle which was carrying its prey.— This remarkable hunt was also observed by Dr. ERIK DAHL, Lund. Later, we have never seen anything like it, and I am sure it was a very rare experience. In the literature I have found a similar case described in SCHJØLER (1931, p. 90) by an experienced observer from Greenland, who also mentioned that it

was his only observation of this kind. Further, LIBBERT (1939) has witnessed a sea-eagle capturing a heron in flight.

2. 1940, Febr. 4. The sea at Falsterbo was mainly frozen, but near the shore there were some stretches of open water with a small flock of mallards (*Anas platyrhynchos*) and a single tufted duck (*Aythya fuligula*). In a heavy squall of snow a sea-eagle suddenly appeared, flying very low. All the mallards managed to leave in time, but the tufted duck remained in the water and dived just when the eagle arrived, but after a rather short hunt it was caught.

It might be said that the tufted duck did not react as fast as usual, and that, moreover, it was the only one of its kind on that particular spot, whereas there were small flocks of the same species in the holes in the ice nearby. The tufted duck is usually social on migration and hibernation. However, for several reasons it is impossible to quote this instance as a selective hunting. The diving ducks often dive rather than fly off, and the specimen may have been under water quite incidentally just when the eagle arrived.

3. 1947, Oct. 16. In the shallow water at Ottenby, the southernmost point of Öland, there were thousands of ducks. Two sea-eagles, one adult and one juvenile, were flying over the bird flocks, looking for prey. Finally, the adult attacked a duck which was injured and unable to fly. The hunt was successful, and the eagle carried its prey to a sand-bank and started eating.

Discussion of the hunts.

My general impression, corroborated by the figures given in Table 4, is that *Haliaeetus albicilla* must work hard for its food. The percentage of successful hunts is equal to 5, but this figure is, of course, derived from the completed hunts, and, as stated above, the sea-eagle usually will not proceed so far; in the great majority of cases the intended prey will escape before the hunt has started! Taking these cases, too, into consideration, it seems obvious that most specimens with normal behaviour and agility will escape. I admit that my observations of successful hunts are too few to permit of a statistical treatment, but they are in agreement with the argumentation.

This statement should of course not be carried too far. In the case of the mallard quoted above I can see no reason speaking in favour of a selective effect, and the same probably often holds true of the capture of ducklings and young birds in the summer.

Fairly often I have witnessed the sea-eagle attack injured birds. Thus, a single *Anser fabalis* which was incapable of flight was violently attacked by an old sea-eagle. The goose, however, defended itself by beating with its wings and was not seized.—

In November, 1947, an injured curlew (*Numenius arquata*) stayed at the

Ottenby meadows for some time, As almost all curlews leave Sweden before October, the observation in itself strongly suggested that the bird was not well. And, as a matter of fact, the hurt was easily detected: one wing was deformed and, when at rest, was trailing on the ground. In flight the curlew kept its body very crooked and asymmetric, but nevertheless it was frequently seen on the wing. This particular specimen was eagerly pursued by the young sea-eagles, and I watched two hunts in detail. The first time, the curlew flew past a roosting eagle at a very considerable distance, but the eagle immediately started hunting and continued its attacks for a long time, until both birds disappeared. Apparently, the eagle was unsuccessful, as I met with the curlew the following day, and now a most remarkable hunt was seen. The curlew got frightened and took wing, when the eagle passed by at a distance, and then the hunt started instantly. It proceeded for a very long time over the flat meadows. The distance between the birds gradually diminished, and finally the eagle was quite close to the curlew, which apparently was now in a very dangerous position and turned and twisted without getting rid of its pursuer. The eagle had turned its talons forwards, widely spread out. After a very long hunt, both birds hurled down behind some high trees and disappeared. Since the final result was not seen, the hunt has not been included in the table, but it is reported here since it seems to be of interest. Almost all birds rise when a sea-eagle is approaching. In such cases the eagle will not normally engage in a hunt. The very fact that the birds rise at a distance usually means that they are no longer prospective victims; the eagle shows no interest in them. But in this particular case the frightened bird had a conspicuous injury, and then the eagle reacted in a perfectly opposite manner, instantly and with a remarkable intensity and perseverance.

S U M M A R Y

1. The present investigation is based on field observations made by the author in southern Sweden, mostly Scania (Skåne), in the years 1942–1947.
2. A statement is given of the reactions of birds of prey to their prospective victims, and vice versa. The concept of hunts is discussed, and it is attempted to give a definition of what can really be considered a hunt.
3. Four species of predatory birds, viz., Sparrow-Hawk (*Accipiter nisus*), Merlin (*Falco columbarius*) Peregrine Falcon (*Falco peregrinus*), and Sea-Eagle (*Haliaeetus albicilla*), are discussed as to their modes of hunting and choice of prey.
4. The observations were made mostly in the autumn and refer to migrating specimens. The representativeness, merits, and disadvantages of the observations are considered with regard to this point as well as to other sources of error.
5. A description is given of all successful hunts of the species in question, as observed by the author.

6. Particular attention was paid to the effectiveness of the hunts and to the possible selective effect of the predatory birds on the birds hunted. In other words, it is attempted to find the percentage of successful hunts, and the question of what individuals are killed is raised. The results are given in the following table.

Species	(a) Total number of hunts observed	(b) Total number of successful hunts	(c) Number of cases in which injury, ab- normality, or abnormal behaviour was observed in victim	Percentage	
				$\frac{b}{a}$	$\frac{c}{b}$
<i>Accipiter nisus</i>	213	23	5	10.8	21.7
<i>Falco columbarius</i>	155	7	1	4.5	14.3
<i>Falco peregrinus</i>	260	19	3	7.3	15.8
<i>Haliaeetus albic.</i>	60	3	1	5.0	33.3
	688	52	10	7.6	19.2

Further details are to be found in Tables 1-4.

Some corrections are proposed in the text, the most important resulting in a higher figure for the total number of hunts of the sparrow-hawk, rendering the percentage of successful hunts of that species considerably lower. Some other adjustments in both directions are also discussed, but neither of these will change the main points as given in the table above.

As seen from the figures, the percentage of successful hunts is very low throughout, in spite of the modes of hunting being different in all four species examined. On the other hand, the number of inferior prey is decidedly high in relation to the percentage of injuries and abnormalities usually seen in birds in the field.

7. From the observations it is concluded that the predatory birds exert a selective influence on the stock of animals, from which they get their prey. Injured or abnormal prey is caught remarkably often, much more often than would be expected from the percentual number of such specimens seen in the field under usual conditions. This does not mean that the birds of prey solely or even mainly catch birds which are in some respect inferior or abnormal. There is evidence that many hunts are successful by mere chance. It is even possible that several species of predatory birds have different modes of hunting, which have no selective effect. Some of these cases are discussed. These methods, however, are not often used, and it is even doubtful whether they are more successful than other methods. The general conclusion is not influenced by these modes of hunting.

8. The conclusions drawn by the present writer are not new; in fact, they have been set forward very often and have been much discussed. The selective effects is considered quite self-evident by some authors, by others it is very much doubted or frankly denied. Most people interested in the subject base their opinion on an unsatisfactory evidence. The relevant data published, be it in hunters' magazines or in modern handbooks, lay too much stress on untypical and unusual cases and thus cannot be used for an analysis. Apparently no figures suitable for a statistical treatment of the subject have been published.

As the present writer has had the opportunity to see a large number of hunts, performed by different species of birds of prey, he considered it justified to publish and discuss these observations. He is, however, fully aware that much work remains to be done in this field.

9. The percentage of injured and abnormal specimens in an animal population is apparently difficult to find out. HICKEY (1943, from other sources) in one case gives the figure 5.35 percent. The figure is a result of a careful examination of 10,000 starlings (*Sturnus vulgaris*), but it is stated that it refers to "the more conspicuous abnormalities" only. Of course there are all gradations between normal and abnormal. Even the most thorough investigation will not reveal all abnormalities in behaviour and psyche. On the other hand, it is obvious that field-studies alone cannot decide the question. Thus I cannot give any figures concerning the "real" percentage of abnormalities. It is, however, justified to conclude from the number of deficiencies observed in the field (1) in birds hunted and caught by predatory birds, and (2) in birds seen in other circumstances.

10. It should be noted that the discussion and conclusions given above refer to birds hunted by other birds. The writer is inclined to believe that the same conclusions hold true as to predator-prey relations between higher animals in general. I admit, however, that this is only a supposition. The corresponding relations between vertebrates and invertebrates, on the other hand, are almost certainly of a different kind. When observing birds hunting insects I have been impressed by the very high number of successful hunts. On several occasions I have seen *Falco subbuteo* catch dragon-flies of the genus *Aeschna* and the birds only rarely missed their prey. In South Africa I watched *Falco naumanni* and *Falco vespertinus amurensis* preying on swarming termites. Sometimes the birds as well as the insects appeared in large numbers. I kept a careful watch and witnessed a large number of hunts, but the birds never missed their prey. In such cases there is almost certainly no selective effect. The level of organization in insects is very different from, and in most respects much lower than, that of vertebrates. Thus I should think that there is a selective effect when insects prey upon other insects, but when hunted by vertebrates the insects are, in my opinion, not equal to the situation. A closer investigation on these questions may be difficult to perform, but most probably would yield interesting results concerning the synecology of animals, the rôle of predators in exerting selection pressure, and the evolution within different groups of the animal kingdom.

TABLES

Successful hunts are given in brackets.

In the first part of this paper (Oikos 1950, p. 77 and 79) I referred to table 1, 2, and 3 as giving particulars of the hunts of the sparrow-hawk, *Accipiter nisus*. It has, however, been necessary to give all particulars concerning these hunts in one table, viz., no. 1. The tables 2-4 refer to *Falco columbarius*, *Falco peregrinus*, and *Haliaeetus albicilla*, respectively.

Table 1. A survey of the hunts of *Accipiter nisus* (L.).

Species hunted	Attacks from a short distance; chase of short duration; prey often, but not always, taken by surprise	Chase of longer duration	Long powerful stoop	Horizontal attack from a long distance	Mobbing	Total number of hunts	Number of successful hunts
<i>Corvus corone cornix</i>	1	1			3	5	
<i>Pica pica</i>	1					1	
<i>Sturnus vulgaris</i>	> 22 (3)	2 (1)	1			> 25	(4)
<i>Carduelis spinus</i>	4		1			5	
<i>Carduelis cannabina</i>	3					3	
<i>Carduelis flavirostris</i>	10					10	
<i>Carduelis sp. ind.</i>	2					2	
<i>Loxia curvirostra</i>	1					1	
<i>Fringilla coelebs</i>	3 (2)					3	(2)
<i>Emberiza citrinella</i>	1 (1)	1				2	(1)
<i>Emberiza schoeniclus</i>	1					1	
<i>Passer domesticus</i>			1			1	
<i>Passer montanus</i>	1					1	
<i>Alauda arvensis</i>	2	1				3	
<i>Anthus trivialis</i>	3					3	
<i>Anthus pratensis</i>	1		1			2	
<i>Anthus spinoletta</i>				1		1	
<i>Motacilla flava</i>	> 14					> 14	
<i>Motacilla alba</i>	3					3	
<i>Motacilla sp. ind.</i>	4		1	1		6	
<i>Parus coeruleus</i>	1					1	
<i>Regulus regulus</i>	3 (1)	1 (1)				4	(2)
<i>Phylloscopus sp. ind.</i>	1					1	
<i>Turdus viscivorus</i>				1		1	
<i>Turdus ericetorum</i>	13 (4)	1		1 (1)		15	(5)
<i>Turdus musicus</i>		1 (1)				1	(1)
<i>Turdus merula</i>	1 (1)					1	(1)
<i>Oenanthe oenanthe</i>	5 (1)					5	(1)

Table 1 (continued).

Species hunted	Attacks from a short distance; chase of short duration; prey often, but not always, taken by surprise	Chase of longer duration	Long powerful stoop	Horizontal attack from a long distance	Mobbing	Total number of hunts	Number of successful hunts
<i>Saxicola rubetra</i>	1					1	
<i>Phoenicurus phoenicurus</i>	1 (1)					1	(1)
<i>Hirundo rustica</i>	3 (1)	1	1			5	(1)
<i>Hirundinidae sp. ind.</i>	1					1	
<i>Small Passeres spp. ind.</i>	> 45 (4)		1	1		> 47	(4)
<i>Columba palumbus</i>					1	1	
Flock <i>Columba pal. + oenas</i>			1			1	
<i>Calidris alpina</i>	1	1				2	
Flocks of small waders	7			1		8	
<i>Larus ridibundus</i>		1				1	
<i>Perdix perdix</i>	1					1	
<i>Falco peregrinus</i>					3	3	
<i>Falco columbarius</i>		1				1	
<i>Falco tinnunculus</i>	2	1			12	15	
<i>Milvus milvus</i>	1					1	
<i>Circus cyaneus</i>					2	2	
<i>Circus aeruginosus</i>	1					1	
Total	> 165	13	8	6	21	> 213	(23)
Total less attacks on "inadequate" prey	161	11	8	6	4	190	(23)
Successful	(19)	(3)	(0)	(1)	(0)	(23)	(23)

Table 2. A survey of the hunts of *Falco columbarius* (L.).

Species hunted	One stoop from a short distance, and/or attack by surprise	More than one stoop, but from a short distance; hunt usually giving impression of short, exciting chase	Several or many clearcut stoops from a short or medium distance; hunt of (rather) long duration	One long powerful stoop	Horizontal attack from a long distance	Mobbing	No details as to mode of hunting	Total number of hunts	Number of successful hunts
<i>Corvus corone cornix</i>	2					3		5	
<i>Pica pica</i>						1		1	
<i>Sturnus vulgaris</i>	3						1	4	
<i>Carduelis spinus</i>	3		2					5	
<i>Carduelis cannabina</i>	1							1	
<i>Carduelis flavirostris</i>	2							2	
<i>Carduelis sp. ind.</i>	1	1	2					4	
<i>Fringilla coelebs</i>	1		1 (1)					2	(1)
<i>Emberiza citrinella</i>	1							1	
<i>Lullula arborea</i>	1		5					6	
<i>Alauda arvensis</i>	2		2 (1)					4	(1)
<i>Anthus trivialis</i>			1					1	
<i>Anthus pratensis</i>	3	1						4	
<i>Anthus sp. ind.</i>		1			1		1	3	
<i>Motacilla flava</i>	7	1 (1)					1	9	(1)
<i>Motacilla alba</i>	3 (1)		2				1	6	(1)
<i>Motacilla sp. ind.</i>	2							2	
<i>Turdus ericetorum</i>	1							1	
<i>Oenanthe oenanthe</i>			1					1	
<i>Hirundo rustica</i>	3 (1)	1	2		1			7	(1)
<i>Riparia riparia</i>		4	1					5	
<i>Hirundinidae sp. ind.</i>	3	1					1	5	
<i>Small Passeres spp. ind.</i>	32 (1)	5	9	1	1 (1)		13	61	(2)
<i>Apus apus</i>		1						1	
<i>Columba palumbus</i>				1				1	
<i>Calidris alpina</i>	1							1	
<i>Small waders spp. ind.</i>	1						1	2	
<i>Falco tinnunculus</i>	1					1		2	
<i>Accipiter nisus</i>	4	1				3		8	
Total	78	17	28	2	3	8	19	155	(7)
Total less attacks on "inadequate" prey	71	16	28	2	3	0	19	139	(7)
Successful	(3)	(1)	(2)	(0)	(1)	(0)	(0)	(7)	(7)

Table 3. A survey of the hunts of *Falco peregrinus* (TUNST.).

Species hunted	Racing, catching by surprise, horizontal attack	One stoop from a short distance	One stoop from a medium distance	One stoop from a long distance	One stoop; no further details available	Stoop repeated 2-5 times	Stoop repeated 6-15 times	Stoop repeated more than 15 times	Number of stoops not noted	Mobbing and "playful" attacks	No details as to mode of hunting	Total number of hunts	Number of successful hunts
<i>Corvus corone cornix</i>	1 (1)						1		2	19		23	(1)
<i>Corvus corone corone</i>										1		1	
<i>Corvus frugilegus</i>			1	1		1	3 (1)		1	1		1	(1)
<i>Corvus monedula</i>												7	
<i>Corvus sp. ind.</i>			1									1	
<i>Pica pica</i>						1						1	
<i>Sturnus vulgaris</i>	5		5	7 (1)	1	13 (2)	1		7	1	4	44	(3)
<i>Carduelis sp. ind.</i>			1									1	
<i>Alauda arvensis</i>			1	1		1						3	
<i>Anthus sp. ind.</i>			1									1	
<i>Motacilla flava</i>	1 (1)											1	(1)
<i>Motacilla alba</i>		1										1	
<i>Motacilla sp. ind.</i>									1			1	
<i>Small Passeres spp. ind.</i>		1	1	1		1					1	5	
<i>Ardea cinerea</i>										1		1	
<i>Anser fabalis</i>				1	1					1		3	
<i>Anas platyrhynchos</i>	2			1			1					4	
<i>Anas crecca</i>		1					1					2	
<i>Spatula clypeata</i>						1						1	
<i>Columba oenas</i>	7		6	2		5 (1)			2	1	1	24	(1)

Table 3 (continued).

<i>Columba palumbus</i>	2 (1)	1 (1)	4 (2)			3	1		2	2		15	(4)
<i>Columba oenas</i> or <i>palumbus</i>	7 (1)		7 (2)	2	1	2			1		3	23	(3)
<i>Columba livia</i> "domestica"			1									1	
<i>Philomachus pugnax</i>						1 (1)						1	(1)
<i>Tringa totanus</i>								1				1	
<i>Tringa erythropus</i>	1											1	
<i>Tringa nebularia</i>										1		1	
<i>Tringa glareola</i> (?)								1 (1)				1	(1)
<i>Vanellus vanellus</i>						2	1	1		1 (1)		5	(1)
<i>Small waders</i> spp. ind.	1		1	1			1		1			5	
<i>Sterna</i> sp. ind.										1		1	
<i>Larus ridibundus</i>	1									1		2	
<i>Larus canus</i>							1					1	
<i>Larus marinus</i>			1							1		2	
<i>Larus</i> sp. ind.										3		3	
<i>Stercorarius parasiticus</i>						1						1	
<i>Falco tinnunculus</i>	1 (1)									5		6	(1)
<i>Buteo lagopus</i>										1		1	
<i>Buteo buteo</i>		2								3		5	
<i>Pernis apivorus</i>										1		1	
<i>Circus cyaneus</i>										5		5	
<i>Accipiter nisus</i>		5	1			1				13 (1)		20	(1)
<i>Haliaeetus albicilla</i>		1										1	
<i>Undetermined birds</i>			5		7				1		9	22	
<i>Nyctalus noctula</i>			7	2								9	
Total	29	12	44	19	10	33	11	3	18	63	18	260	(19)
Total less attacks on "inadequate" prey	29	9	44	19	10	33	11	3	18	58	18	252	(19)
Successful	(5)	(1)	(4)	(1)	(0)	(4)	(1)	(1)	(0)	(2)	(0)	(19)	(19)

Table 4. A survey of the hunts of *Haliaeetus albicilla* (L.).

Species hunted	Attacks, often repeated and of long duration, against flocks of birds on water	Attacks, usually repeated and of long duration, against single birds on water	Attacks on birds on land	Long, steep stoop against birds on water	Long, steep stoop against birds on land	Persistent pursuit of flying birds	Strike at bird in flight	Total number of hunts	Number of successful hunts
<i>Cygnus cygnus</i>		1						1	
<i>Anser fabalis</i>		1	5		1			7	
<i>Anas platyrhynchos</i>	5						1 (1)	6	(1)
<i>Somateria mollissima</i>		1						1	
<i>Aythya fuligula</i>		1 (1)						1	(1)
<i>Mergus merganser</i>	6							6	
Undet. or mixed flocks of ducks, usually <i>Anas platyrh.</i> , <i>Aythya fulig.</i> and/or <i>Bucephala cl.</i>	25 (1)			1				26	(1)
<i>Fulica atra</i>	9							9	
<i>Larus argentatus</i>						2		2	
<i>Numenius arquata</i>						1		1	
Total	45	4	5	1	1	3	1	60	(3)
Successful	(1)	(1)	(0)	(0)	(0)	(0)	(1)	(3)	(3)

REFERENCES

- Since the first part of this paper was published, some other papers dealing with predation and selection have appeared; these are included below although not referred to in the text.
- BARTH, E. K., 1948: Kongeørnens rolle i naturen. Norsk Jaeger- & Fiskerforenings Tidsskrift nr. 5, 1948.
- BARTH, I. B., 1894: Erfaringer fra jakten paa det mindre vildt i Norge. Kristiania 1894. (Quoted from Brinkmann 1927 b).
- BENT, A. C., 1938: Life Histories of North American Birds of Prey. Part 2. Smiths. Inst., U.S. National Museum, Bull. 170. Washington 1938.
- BERGSTRÖM, U., and SVÄRDSON, G., 1939: Ringmärkningar och fågeliakttagelser vid Ölands Södra Udde under höststräcket 1938. Fauna och Flora 34, p. 100.
- BODENHEIMER, F. S., 1938: Problems of Animal Ecology. Oxford University Press.
- BOND, R. M., 1946: The peregrine population of Western North America. Condor 48 (especially p. 113-115).
- BRINKMANN, A., 1923: Lirypens entoparasiter (The entoparasites of the Willow Grouse). Bergens Museums Aarbok 1921-22, Naturvidensk. række nr. 3. With a summary in English.
- 1927 a: Jagtlovgivning og fredning. Naturen 1927.
- 1927 b: Coccidiosen hos lirypen (The coccidiosis in the Willow Grouse). Naturen 1926.
- DROST, R., 1930: Ueber den Vogelzug auf der Schlangeninsel im Schwarzen Meer. Abhandl. a. d. Gebiete der Vogelzugsforschung 2, Berlin.
- DURANGO, S., 1948: Om jaktmetoder och föda hos några av våra rovfåglar. Svensk Jakt 1948, nr. 5.
- ELTON, C., 1942: Voles, Mice and Lemmings. Problems in Population Dynamics. Oxford University Press.
- ENGELMANN, F., 1928: Die Raubvögel Europas. J. Neumann-Neudamm.
- ERRINGTON, P. L., 1946: Predation and vertebrate populations. Quart. Rev. Biol. 21. (See also discussion of this paper by H.N.S. [i. e. Southern] in Ibis 89, 1947, p. 381-382).
- FERDINAND, J., 1923: Nogle Danske Dagrovfugles Føde. Dansk Orn. For. Tidsskrift 17, IV.
- FÖRTECKNING ÖVER SVERIGES FÅGLAR. Utgiven av Sveriges Ornitologiska Förening 1949. (Check-list of Swedish Birds, published by the Swedish Ornithological Society 1949).
- GEYR VON SCHWEPPEBURG, H., 1929: Zugstrassen-Leitlinien. J. Orn., Ergänzungsband II, Festschrift Hartert 1929.
- 1933: Zur Theorie der Leitlinie. Ardea 22, 3/4.
- 1936: Storchzug und Mittelmeer. J. Orn. 84, 3.
- 1942: Merkwürdiger Jagdflug von Falco columbarius. Ornith. Monatsber. 50, 1.
- GROEBBELS, F., 1932: Der Vogel. Band I. Atmungswelt und Nahrungswelt. Berlin, Gebr. Borntraeger.
- 1951: Noch einmal »Albinismus und Auslese«. Orn. Mitt. 3, p. 265-267.
- HARTERT, E., 1912-1921: Die Vögel der Paläarktischen Fauna. Band II. Berlin.
- and STEINBACHER, J., 1932-1938: Die Vögel der Paläarktischen Fauna. Ergänzungsband. Berlin.
- HICKEY, J. J., 1943: A Guide to Bird Watching. Oxford University Press.
- HOLMSTRÖM, C. T., ET AL., 1944: Våra Fåglar i Norden. Band 2. Stockholm.
- HORST, F., 1951: Albinismus und Auslese. Orn. Mitt. 3, p. 11-13.
- HORTLING, I., 1929: Ornitologisk Handbok. Helsingfors.
- JÄGERSKÖLD, L. A., 1945: Stör ej naturens jämvikt. Sveriges Natur (Svenska Naturskyddsföreningens Tidskrift) 36, nr. 5.

- KALELA, O., 1949: Ueber Fjeldlemming-Invasionen und andere irreguläre Tierwanderungen. Ann. Zool. Soc. Zool.-Bot. Fenn. »Vanamo«, Tom. 13, nr. 5. Helsinki.
- KLEINSCHMIDT, O., 1937: Falco Peregrinus II. Eine zweite Monographie des Weltformenkreises des Wanderfalken. Halle.
- KRAMER, V., 1951: Hoher Beuteanteil von Hausgeflügel beim Habicht infolge fehlender Schutzfärbung. Orn. Mitt. 3, p. 187.
- LACK, D., 1946: Competition for food by birds of prey. Journ. Anim. Ecol. 15, nr. 2.
- LIBBERT, W., 1939: Seedler erbeutet Reiher. Orn. Mber. 47, nr. 6.
- LORENZ, K., 1943: Die angeborenen Formen möglicher Erfahrung. Zschr. Tierpsychol. 5.
- LOWE, W. B., 1940: How do large Raptorial Birds hunt their Prey? Ibis, ser. 14, vol. IV, p. 331-333.
- MEINERTZHAGEN, R., 1940: How do larger Raptorial Birds hunt their Prey? Ibid. p. 530-535.
- MUNTHE-KAAS LUND, H., 1950: Et bidrag til kjennskapen om hønschaukens næring i Norge. Særtrykk av Skogdirektørens Årsmelding 1943-1947. Oslo.
- NIETHAMMER, G., 1938: Handbuch der Deutschen Vogelkunde. Band. II Leipzig.
- NOTINI, G.: vide Svenskt Jaktlexikon.
- OBERLÄNDER, 1907: Raubzeugverteilung und Wildentartung. Kosmos 1907, Heft 3. Quoted from Heilmann, Dansk Orn. For. Tidsskrift 1, 1907, p. 141.
- OMER-COOPER, J., 1948: Report on the Relationship between Predator and Prey. Bull. Soc. Fouad I. Entom., XXXII, 1947.
- PEITZMEIER, J., 1950: Albinismus und Auslese. Orn. Mitt. 2, p. 55-57.
- PETERS, J. L., 1931: Check-List of Birds of the World. Vol. I. Cambridge, Harvard University Press.
- RÖRIG, G., 1909: Magen- und Gewölluntersuchungen heimischer Raubvögel. Arb. Kais. Biol. Anst. f. Land- und Forstwirtschaft VII, 4, Berlin.
- RUDEBECK, G., 1943: Preliminär redogörelse för fågeliakttagelser i Skanör och Falsterbo hösten 1942. Vår Fågelvärld 1943, häfte 1-3.
- 1947: Fåglarnas höststräck över Falsterbonäset. Natur i Skåne, edited by Bertil Hanström och Kai Curry-Lindahl.
 - 1949: Jägaren och rovfåglarna. Skånska Jägarsällskapets Årsbok 1948, Lund 1949. Also in: Sveriges Natur (Svenska Naturskyddsföreningens Tidskrift) 40, nr. 5, 1949.
 - 1950: Studies on Bird Migration, based on Field Studies in Southern Sweden. Vår Fågelvärld, Supplementum I, Lund 1950.
- SCHÄFER, E., 1938: Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. J. Orn. 86, Sonderheft. Berlin.
- SCHJØLER, E. L., 1932: Danmarks Fugle III. Rovfugle. København.
- STEINBACHER, G., 1951: Albinismus. Orn. Mitt. 3, p. 129-131.
- SWANBERG, P. O., 1931: Krankesjön. Stockholm.
- Svenskt Jaktlexikon. Huvudredaktör Gösta Notini. (Swedish Hunting Dictionary. Chief Editor Gösta Notini). Stockholm 1947.
- SVÄRDSON, G., 1948: Verksamheten vid Ottenby Fågelstation 1947. Vår Fågelvärld 7, nr. 1.
- 1949a: Den hemliga döden och rovdjuren. Svensk Jakt 1949, nr. 8.
 - 1949b: Verksamheten vid Ottenby Fågelstation 1948. Vår Fågelvärld 8, nr. 3.
 - 1950: Verksamheten vid Ottenby Fågelstation 1949. Ibid. 9, nr. 1.
- THIENEMANN, J., 1931: Vom Vogelzuge in Rossitten. J. Neumann-Neudamm.
- TILLISCH, C. J., 1949: Falkejagten og dens Historie. København.
- TINBERGEN, L., 1946: De Sperwer als rovfrijand van zangvogels. Ardea 34.
- TINBERGEN, N., 1939: The Behavior of the Snow-Bunting in Spring. Trans. Linn. Soc. New York 5.

- 1951: *The Study of Instinct*. Oxford.
- TISCHLER, F., 1941: *Die Vögel Ostpreussens und seiner Nachbargebiete*. Königsberg (Pr.) und Berlin.
- TÄNING, Å. VEDEL, 1933: *Rovfugletræk ved Falsterbo*. Dansk Orn. For. Tidsskr. XXVII, 2.
- UTTENDÖRFER, O., 1930: *Studien zur Ernährung unserer Tagraubvögel und Eulen*. Abh. Naturf. Ges. Görlitz 31, 1.
- 1939: *Die Ernährung der Deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur*. J. Neumann-Neudamm.
- 1952: *Neue Ergebnisse über die Ernährung der Greifvögel und Eulen*. Stuttgart/z.Z. Ludwigsburg.
- VAN DOBBEN, W. H., 1952: *The Food of the Cormorant in the Netherlands*. Ardea 40 (especially p. 58–59).
- WENKEL, F., 1951: Zu »Albinismus und Auslese«. Orn. Mitt. 3, p. 112.
- WESENBERG-LUND, C., 1929: *Some Features of the Avifauna of Denmark and its present Life-conditions*. Verhandl. d. VI. Int. Orn.-Kongr. in Kopenhagen 1926. Berlin 1929.
- WITHERBY, H. F., ET AL., 1945: *The Handbook of British Birds*. Vol. 3. London.
- WRIGHT, S., 1931: *Evolution in Mendelian Populations*. Genetics 16.
- 1940: *The Statistical Consequences of Mendelian Heredity in Relation to Speciation*. The New Systematics, ed. by J. S. Huxley. London, Oxford University Press.

En stor del av det fältarbete, som ligger till grund för uppsatserna i detta häfte utfördes under åren 1941-1945 på Falsterbohalvön. Vid tiden för den ursprungliga tryckningen hade serien "Meddelanden från Falsterbo fågelstation" ännu ej startats. När arbetet nu trycks i en ny upplaga har det därför bedömts som lämpligt att låta arbetet ingå i Falsterboserien.

Beställningar sker till Skånes
Ornitologiska Förening, Ekologihuset,
223 62 LUND.

Order from: Ornithological Society
of Skåne, Ecology Building, S-223 62
LUND, Sweden.

Andra tryckningen, 1982.