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A preliminary investigation of the Carrion Crow *Corvus corone* problem in Switzerland [1, 2]

Part I. General introduction and population problems

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1. General introduction

The conflict between nature and human interest goes back several centuries. Thus various species of the genus *Corvus* have been recognized around the globe as potential pests to agriculture, forestry and small game management. This is in contrast to other records on their beneficial influence by destroying rodents, insect pests, etc. The argument whether they are our friends or enemies have often been heated, and is yet undecided. The problem has prompted numerous studies to establish the role of crows in their relation to human ecology and economy (KALMBACH 1939, MANSFELD 1953, MEIDELL 1943, ROWLEY 1969, etc.)

The carrion crow *Corvus c. corone* is a species native to Switzerland. Although there had been previous complaints by hunters on crow damage to small game, and ornithological organizations reported the destruction of song bird nests, the problem has become serious only during the past decade. Damage to corn fields by crows (chiefly *Corvus brachyrhynchos*, the common crow) can be considerable on the North American continent (KALMBACH 1939). With the introduction of the corn as agricultural crop to other continents the same problem has arisen in several areas. In Switzerland the corn has become a major crop only during the past decade, coinciding with reports of increasing crow numbers. Meanwhile damage to crops has also been recorded. This recent development has been the main reason for the present investigation.

The causes of the study have also determined its aims. Firstly we must know whether the population increase has been real, and if so, then whether it is related to the introduction of the corn. Furthermore, before crow damage to agriculture and possible methods of control are discussed, it is basic to study the ecology of the species in relation to conditions specific to Switzerland. Without such knowledge our understanding of the problem would be incomplete, resulting in a series of faulty conclusions. Consequently, a preliminary investigation of crow population problems had to be undertaken, and will be reported in Part I of this paper. Part II will deal with damage to agriculture, methods of crow control, and will also contain a general discussion of the problem with certain recommend-

[1] This study was partly subsided by generous financial help from the cantons Aargau, Bern, Luzern, Obwalden, Schaffhausen, Thurgau and Zürich.

[2] Der Wunsch des Verfassers, von einer Übersetzung seines englisch geschriebenen Manuskriptes abzusehen, und die freundliche Bereitschaft der Vogelwarte Sempach, dafür einen wesentlichen Teil der Druckkosten zu tragen, haben uns dazu bewogen, ausnahmsweise einen fremdsprachigen Beitrag aufzunehmen. Der zweite Teil der Studie, dessen Publikation für 1976 vorgesehen ist, wird jedoch in deutscher Übersetzung erscheinen. Red.

ations. The investigation does not pretend to be exhaustive, as two breeding seasons are not enough to answer all the questions. Hopefully it will present the basis for further investigations that would prove or disprove the hypothesis to be given here.

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2. Technical information

2.1 *Study area*

During the first summer the study was confined to an approximately 12 square kilometres area in a broad valley, extending to the west of Sursee in central Switzerland (08°00'—03' East, 47°09'—11' North). It was large enough to hold a sufficient number of crow territories, while being conveniently small to be surveyed by one person on every second day. Its arbitrary boundaries roughly coincided with the national grid to the north, east and south, and were determined by roads and a brook to the west. The villages of Wauwil and Ettiswil were excluded from the area. The valley extended beyond the boundaries in a southwest, northwest and easterly direction, and was surrounded by partially forest covered hills to the north, west and south-east.

The flat central part of the study area was characterized by intensively cultivated land belonging to the State Penal Farm, and lined by drainage canals, farm roads and rows of trees and shrubs forming a network. The surrounding areas were owned by individual farmers. Farm buildings with small orchards were typical and sporadic in distribution. Larger groups of trees were situated only at two places, with a total area of ca. 4 ha of conifer woods. A larger patch of forest, abouth 0.2 square kilometre, was located just outside the eastern boundary of the area (Chalpecherwald). The landscape was sligthly undulating towards the south and north-west and to the west. Isolated trees over the farm lands were common.

Formerly dominated by marshes, mostly drained by now, the land is primarily agricultural today. About a third is used for grazing and hay, the latter regularly cut throughout the growing season. Among the cereals grown the corn is a major crop. Vegetables, potato fields and small orchards around the houses made up the rest.

The study was extended to the hills just south-east of the area following the 1973 summer, covering about 6.5 square kilometres. Just over half of it was mixed woods, Open areas in small valleys, around isolated farms and small settlements were restricted. Pastures and orchards were very common here, while corn was virtually absent and other cereals were also infrequent.

2.2 *Study methods*

The study of population ecology is not just a matter of recording changes in numbers. This is particularly true in the case of species with complex social structure, as the crow. The knowledge of the fate and interaction of individuals within a population may reveal important determinants that can be overlooked otherwise. Thus the use of colour marking, etc. for individual recognition would be basic to investigation of this kind. The mass marking of crows can be done either trough trapping, or in the nest. As trapping depends on deep snow when the groups can be lured by baiting, all efforts were failures as both the 1972/73 winter, just preceding the study, and the 1973/74 season were characterized by the complete absence of snow. During the 1973 summer only two broods could be banded, as most of the nests were difficult to reach, technical assistance was missing, and many nests were destroyed within the study area.

The only possible way to overcome this difficulty was to check the population as frequently as it could be done. With such an intensive survey two alternatives were avail-

able. Some sections of the population might have been observed over a long period of time, for example a full day, to note all important events, then switching to another group of territories the next day. With this method accurate information would have been available for a number of pairs, leaving the rest of the population unchecked for a while. As it was found that quick and important changes could occur within a day, particularly during the territorial and breeding seasons, the alternative method of quickly checking the entire population daily or every second day was choosen. Thus during two springs and summers the territorial pairs and group areas were checked nearly every morning and afternoon, including even weekends during the second year. Throughout the autumn and the 1973/74 winter these checks decreased to 2 to 3 per week. Although very much essential information on social interactions, etc. was missed because of the lack of marked birds, the frequency of surveys gave a very good knowledge of the territorial birds, and changes in status, nest desertions, renestings and other aspects could be recorded.

Breeding success was checked both directly, by the control of a number of nests, and indirectly, by observing the number of newly fledged young on all occupied territories during the 1973 season. In 1974 the study was extended into the hills, where nests in the forest were practically impossible to find. Furthermore, as many of the nests were destroyed by farmers in 1973, bringing unwarranted attention to nest-sites was not desirable. Therefore in the second year the indirect method of counting all fledged young was applied. The young normally remain on the territory for a long period of time, often throughout the winter, and are easily observable on the fields in the company of parents. As the main reason to check breeding success was to compare the productivity of plain and hill populations, and the number of fledged young per territory was an applicable index, this method proved satisfactory under the circumstances.

3. Demographic data

3.1. *Breeding population*

The density of the population within the study area was measured as the number of breeding territories present. It remained constant at 36 both in 1973 and 1974. Some of these territories were marginal, with part of the utilized area outside the study boundaries (Figs. 1, 2). They were included in the population only, if the pair and the young, if any, spent most of their active time within the study area, regardless of the position of the nest. Boundaries of the territories seemed to be loose and in the majority of the cases neighbouring pairs were not in close contact with one another. This presumably depended to a large extent on the position of suitable nesting sites and other aspects of the habitat, as frequent territorial fights early in the breeding season indicated that all space was taken up by breeding pairs in both years. In general breeding territories were closely packed in orchard areas and more sparse where trees were less frequent. The presence of non-territorial social groups might have affected nesting densities as well (Section 3.2).

Because of the loose boundaries, territory size measurements were omitted. The density of the breeding population could be expressed simply as the number of pairs per square kilometre, which was approximately 3 in both years. This may indicate a relatively low population density for Switzerland, as WACKERNAGEL (in GLUTZ VON BLOTZHEIM 1962) claims an average of 5 breeding pairs of carrion crows in the central low lands and the Jura regions, with a range of 3 to 6. A more exact way of comparison can be achieved by using the 'nearest neighbour distance' that gave an average of 353 m in the Wauwilermoos area in 1973. This compares well with other Swiss studies and classifies as a moderately 'high' population density on WITTENBERG's density scale (1968) devised for German conditions (Table 1).

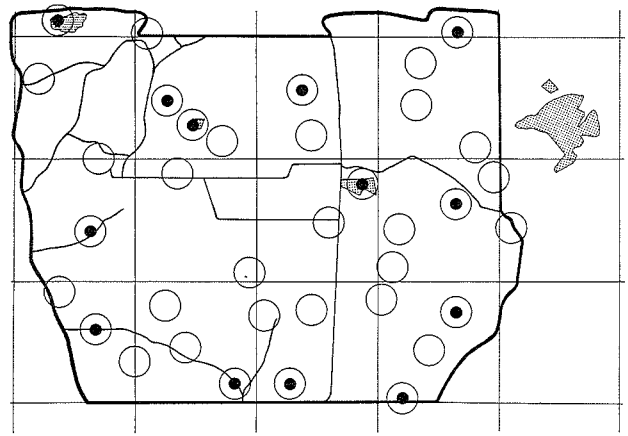

FIGURE 1. Breeding territories (circles) within the Wauwilermoos study area in 1973. The grid coordinates indicate square kilometres, the dotted areas are forest patches used as roosts. Solid circles represent pairs with fledged young.

The adult breeding population was 72 during the period of the study. However, both in 1973 and 1974 a family 'triangle' was observed on two territories, raising the total to 74. In the absence of individual marking it could not be determined whether these extra birds represented polygamy or social helpers. WITTENBERG (personal communication) observed even three year old individuals still on their parental territory, although these may be forced out of the territory once sexually matured and exhibiting signs of territorial behaviour.

Exact population numbers were extremely difficult to determine in the forested hills due to the changing terrain interrupted by extensive woods, where the status of unmarked individuals could not be established with certainty. In all 24 territories could be recognized through observations in early spring and during the breeding season (Fig. 3), and the existence of 3 additional breeding pairs was suspected in the most inaccessible areas. Thus over the total area of 6.5 km² the minimum density of the breeding population was 3.7 per square kilometre, and the suspected maximum 4.1, the latter being significantly higher than the density in the agriculturally intensive valley where the Wauwilermoos area was situated.

In both areas the territories persisted throughout the year, although a few became deserted for unknown reasons. During the winter several pairs appeared

TABLE 1. Comparison of population densities of the carrion crows from different parts of Switzerland, using the classification of WITTENBERG (1968) in Germany based on the average nearest neighbour distance.

Locality	n	Density levels			Authors
		moderate	high	very high	
Germany	—	450 m	450—200 m	200 m	WITTENBERG 1968
Wauwilermoos	33	—	353	—	present study
Les Grangettes	15	—	368	—	GILLIÉRON (unpubl.)
Maschwanden	13	—	290	—	BÜHLER (unpubl.)

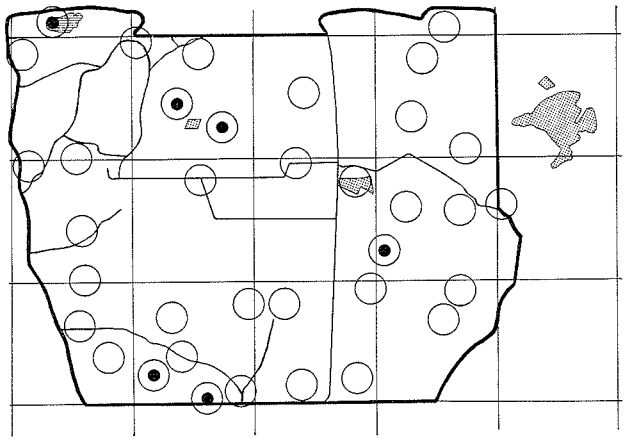

FIGURE 2. Breeding territories and successful breeding pairs in the Wauwilermoos area in 1974. For explanations see Figure 1.

to leave their territories in the evenings and joined the communal roost for the night, a phenomenon reported by WITTENBERG (1968) as well.

3.2. *Social non-breeders*

In addition to the breeding population a substantial number of non-breeders were regularly present in the Wauwilermoos area throughout the study period. These birds stayed in social groups of varying sizes which occasionally joined one another on the feeding grounds. The overall number of social birds did not stay constant, but varied with the season. In both years there was a characteristic increase in April and May over what appeared to be a 'base' level, and to which level the numbers declined again by early June (Fig. 4). In 1974 both this base level and the spring increase was much more pronounced, resulting in a non-breeding population within the area that exceeded 200 individuals at its peak in

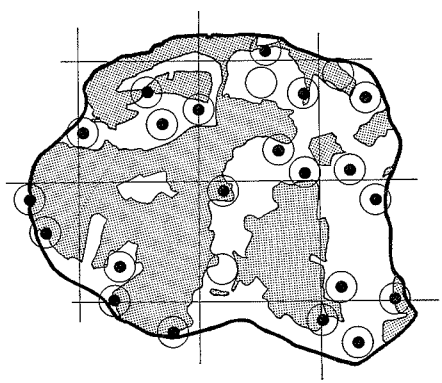

FIGURE 3. Breeding territories, indicating successful pairs, in 1974 in the woodland area of the adjacent hills. For explanation see Figure 1.

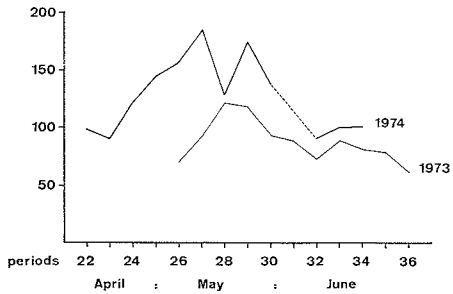

FIGURE 4. Changes in the number of social non-breeders during the 1973 and 1974 seasons in the Wauwilermoos area. Five days averages are calculated in accordance with standardization of the representation of ornithological data (BERTHOLD 1973).

May, in contrast to the highest figure of 164 birds counted on a single occasion in May 1973.

This 'basic' social group belonged to the traditional night roost of Chalpecherwald situated along the eastern boundary of the study area, which was also utilized by other groups normally feeding in other parts of the valley. The April and May increase in numbers was the result of an influx of groups from the outside, chiefly from the surrounding hills, which was easily determined through observations of group movements. As far as it could be established in the absence of a marked population, these visiting groups returned to their usual roosts for the night. The distribution of social groups within the study area is described in more details in Part II of this paper. The breeder to non-breeder ratio was roughly 1 : 1 in 1973 and 1 : 3 in 1974, indicating the increase in the number of social birds in the second year. These figures are taking only the pre- and post-breeding 'basic' level of social birds into calculation.

Following the 1973 breeding season numbers in the social groups remained level throughout the summer, and then increased to about 80 to 90 birds in August and September when the young of the year gradually left their parental territories. This process was also observed in Scottish populations (PATTERSON, personal communication). It was suspected, however, that the young often joined their parents, and such bonds might have persisted until the next breeding season. At least three families stayed together for most of the winter.

Population numbers in the groups exhibited erratic changes over the winter season. In late September over 170 birds were present, and during November and December they fluctuated between 170 and 250. Exact figures were very difficult to determine. The causes of these fluctuations remained unkown, although an apparent correlation with weather conditions existed. Numbers generally increased during cold spells, especially when wet snow covered the surrounding hills. Like during the breeding season, the winter increase was the result of crows coming to the valley from the neighbouring forested regions. It is presumed, although not verified in the absence of marked birds, that under extremely bad weather conditions the visitors included territorial pairs from the hills which joined both the feeding groups and the night roost temporarily.

After January there was an obvious decrease in the number of group birds, staying between 100 and 150 in February. In May and early April there was again an erratic fluctuation, presumably in relation to weather and social factors. On cold or rainy days the groups were larger and more apparent, while on warm and sunny days they were dispersed, broken into smaller groups and even individual pairs. Social interactions were observed daily, involving wandering

pairs and established territorial birds. The number of pairs observed during this period was not fixed, although it was considerably higher than the final number of breeding territories in May.

In the absence of marked birds the exact determination of age and sex distribution within the social groups remained impossible. The evident presence of pairs within the groups in fairly high numbers, and their interaction with resident pairs, indicated a high proportion of sexually mature individuals. This would confirm the findings of CHARLES (unpublished manuscript) for Scottish populations of the carrion crow, where during the breeding season replacement of a pair may occur within a few hours, indicating a population surplus of sexually mature birds mated within the goup. Some of these birds were evidently at least five years old. WITTENBERG (1968) thought that most of the group individuals were immatures, but this may either reflect a special situation or a bias in the absence of a marked population. According to KALCHREUTER (1971) none of the first year, and only about 25 % of the second year birds took part in breeding in Germany, although the latter were sexually mature and exhibited signs of breeding behaviour. Autopsy examination of specimens kept at the Vogelwarte indicated that approximately 20 % of the group individuals at the start of the breeding season were first year birds, based on ovary, oviduct and testis conditions, and also on plumage characteristics. The true percentage was probably somewhat higher, and BÖHMER (unpublished manuscript) gives 30 % as the proportion of one year old birds in May within the Swiss carrion crow population. An extensive banding program would be highly desirable to arrive at accurate figures. Accepting the above information as 'circumstantial' evidence, it seems that a considerable proportion of the social groups during the breeding season are of older ages at times in pairs, but unable to breed for lack of space or for other reasons.

Apart from roosting in woods adjacent to broad agricultural areas, social groups were totally absent from the forested hill areas. Small groups of 3—6 individuals seen there in late summer and during the autumn were family groups. In addition a social group of 25—30 individuals were regularly seen in the easternmost section of the hill study area in May and June 1974, where forest was absent and only rows of trees interrupted a broad agricultural zone.

3.3. *Productivity of the population*

During the 1973 breeding season 12 nests were checked in the Wauwilermoos area, representing just one third of the breeding population, and the results are given in Table 2. Clutch size was determined for nine nests only, averaging 4. 11, somewhat lower than in Finland (TENOVUO 1963) and Braunschweig (WITTENBERG 1968), presumably reflecting latitudinal differences. Bad weather causing a delay in laying and repeat attempts were also responsible. This average nevertheless falls within the range reported from various parts of Britain (HOLYOAK 1967). As the nests could not be checked often enough, the average brood size of 3.38 from eight nests during the second half of the nestling period can neither indicate hatching success nor can it be used to calculate nestling mortality. However, this mean may indicate fledging success as the first two weeks of the nestling period are the most critical for the young and after that survival greatly improves (HOLYOAK 1967, TENOVUO 1963). Thus nestling survival may be somewhat higher here than in Finland with a range of 2.62—3.38 depending on locality,

TABLE 2. Breeding data of crows from twelve nests for the 1973 season.

Nest	Eggs	Nestlings	Fledglings	Remarks
1	4	4	0	robbed
2	4	3	3	—
3	?	1	0	robbed
4	3	0	0	destroyed
5	4	3	0	destroyed
6	4	4	2	—
7	5	5	5	—
8	5	5	0	? ?
9	3	0	0	destroyed
10	?	0	0	robbed
11	5	?	0	destroyed
12	?	2	2	—
n	9	8	12 (4)	
total	37	27	12	
mean	4.11	3.38	1.0 (3.0)	

where according to TENOVUO food conditions for the young are strenuous. As only four of the pairs under control could produce fledging young, the failure rate was 0.67 with a mean 3.0 young per successful pair and 1.0 young for the total breeding population. These figures can be accepted as true for the entire population, as young out of the nests could be easily seen with their parents feeding over the fields. Thus slightly over one third of all pairs (13/36) within the study area fledged at least one young, with a total of 33 fledglings for the breeding population. The mean number of young per pair was 0.91, slightly lower than the observed rate from the pairs under control. However, allowing for a margin of error by missing one or two young on the fields, the productivity of the population was just about 1.0 young per breeding pair.

In 1974 the low breeding success was accentuated, as only six pairs out of 36 could fledge young, with a failure rate of 0.8. As nest destruction by people in 1973 was influenced by the nest control, the 1974 data were collected by observing the pairs twice almost every day, and keeping an eye on young with the parents. In all 17 young were observed, 2.83 per successful pair, somewhat lower than in the previous year. With a possible margin of error, as explained above, the difference was presumably less. However, the year was extremely bad for the entire breeding population, with a productivity of 0.47 young per pair.

The underlying reasons are complex. Practically all nests failed both seasons which were situated within the communal group feeding areas indicating strong social pressure and perhaps even nest robbery by non-breeders. At least two nests were deserted during the incubation stage in 1974 following continuous interference by neighbouring magpies *Pica pica*. The same year a minimum of two nests failed due to predation by the common buzzard *Buteo buteo*, as shown by their activity in the nesting trees, the excitement of the parents and the subsequent desertion of the nests, although not of the territories. Nevertheless, human interference was by far the major cause of nesting failure in both years within the Wauwilermoos area. Several nests were completely destroyed, being pushed off the trees. A bounty hunter was visiting parts of the area shooting at nests, and the cut off legs of nestlings dead under the trees provided evidence of his success.

Children probably robbed several nests that were easily accessible and obvious in single trees along roads and in orchards.

Very low productivity was also reported by WITTENBERG (1968) from two populations in areas of intensive agriculture of Germany, with 1.2 fledged young per pair over a five year period (ranging from 0.7 to 1.7), and with a mean nesting failure of approximately 0.8. There small patches of woods provided both roosts to the flocks and nesting sites to the breeding pairs, and social pressure was presumably a critical factor. In Finland hunters are mainly responsible for low breeding success of crows, by destroying nests in the archipelago where crow predation on duck eggs and ducklings is a potential menace to small game hunting (TENOVUO 1963). HOLYOAK (1967) also considers human interference with crow breeding considerable in Britain.

The low productivity reported here and from Germany, Britain and Finland reflects the situation in areas where crows compete directly with human interests. However, the woodland population in the adjacent hills in the almost complete absence of human interference produced a drastically higher breeding success in 1974. Although the difficult forest covered terrain made exact observations impossible, and a number of young and presumably some families were completely missed, 21 pairs were seen with fledged young out of a total of 24 observed pairs, indicating a maximum failure rate of 0.13. Considering a margin of error the situation was presumably better. This error was affected to a large extent by crow scare devices using pre-set explosive charges in the cherry orchards among the hills, coinciding with the post-fledging period. Families were extremely cautious keeping most of the time close to the forest edge, and often only one or two members of a family could be seen in the open. Even with such shortcomings 44 young were seen with certainty on 16 territories, with a mean of 2.75 per pair. On the remaining five successful territories the number of young could not be determined as the families were never seen completely out in the fields. Projecting the observed figures for the entire hill population of 24 known pairs the productivity was 2.4 young per pair. However, it is very possible that some families were completely missed, and also, that the three 'unsuccessful' pairs were simply not observed with their young, as their territories were over woodlands to a major extent. Furthermore, even for the known families the missing of a few young should be taken into calculation. Thus the above mean represents only a minimum productivity rate for the woodland population, but in reality it was presumably exceeding 2.5 young per pair.

3.4. *Survival and population turnover*

Because of the shortage of time and in the absence of a banded population the calculation of age distribution, mortality rates and a life table was impossible. Thus the estimation of a population turnover is essentially speculative and relies on circumstantial evidence and reports from other authors.

The breeding population in the Wauwilermoos area stayed at the same level during the two years of study, with 36 breeding territories. Throughout the 1973 summer and the subsequent winter season 28 resident pairs stayed on their territories with no apparent discontinuity. Unobserved mortality is very unlikely, as replacement outside the territorially most active pre-breeding period can hardly be immediate. Even one of the previously mentioned 'triangles' survived on one territory. This would require a 78 % adult survival for the

territorial population and may even be higher, as even if mortality had been the cause for the temporary or permanent disappearance of the remaining 8 pairs, it presumably meant the death of only one of them, at a given time. — Only six nestlings could be colour banded in 1973, and four of these survived until the 1974 breeding season on their parents' territories. There were indications of fairly high survival even among the unmarked young within the area. Mortality within the social groups was impossible to estimate. This apparently high adult and first year survival might have been caused by the relatively good weather conditions during the 1973/74 winter, with snow being absent most of the time even from the hills, and when present, staying for only a few days or even less. There was no evidence of food shortage during the winter, an assumption supported by the fact that corn spilled over the ground and standing on the fields was not much utilized by the groups (TOMPA 1976). This confirms the claim by HOLYOAK (1971) that most adult mortality in crows in Britain is not food related, but may be affected by social pressure and territorial contests in late winter and early spring.

Reports by other authors on crow mortality rates are rather conflicting. Unfortunately HOLYOAK's figure for first year mortality is based on the calendar year and therefore it is difficult to use for comparison. Nearly 40 % of the young die until the end of December and a very high percentage during the first four months of the following year. BUSSE (1969) calculated an average 62.4 % first year mortality for European carrion crow populations. As it compares well with the rates given for closely related species (ROWLEY 1971), it will be provisionally accepted in the present paper as basis of calculations. Usable adult mortality rates are more difficult to arrive at. HOLYOAK (1971) records an approximately 52 % annual mortality rate for British and Finnish crow populations. KALCHREUTER (1971) speaks of a 'high' mortality of 41 % among German crows under heavy human persuit, while BUSSE calculated a nearly three years average life expectancy for European crows surviving until their second year of life. This would require an annual mortality of ca. 20 %. The latter conflicts strongly with the situation reported from Britain, although in Scotland survival of territorial pairs is claimed to be 'very high' (PATTERSON, personal communication). It should be added, that adult males of Australian corvid species had a low mean annual mortality of 15—25 % (ROWLEY 1971).

A simple tabular calculation based on a 62.4 % first year and a 50 % second year mortality, with annual adult mortality and the productivity of the breeding population of 50 pairs being the only two variables, may help to dissipate some of the confusion and to understand the problems of population turnover in the two study populations (Table 3). It is clear, that the two populations with an annual productivity of 1.0 and 2.0 fledged young per participating pair would rapidly decline to extinction, even with a 20 % adult mortality rate. Even at a 2.5 young per pair productivity a low 20 % adult mortality would be required to have enough second year birds to produce any population surplus of sexually mature individuals. Thus the German populations with the reported rates of productivity and mortality rates (KALCHREUTER 1971, WITTENBERG 1968) are not able to sustain themselves, while the British and Finnish populations, based on the mortality rates given by HOLYOAK (1971), would require slightly over 6.0 fledged young pair breeding pair. As the maximum mean clutch size in Britain is 4.1 (HOLYOAK 1967), some gross error must be concealed either in the

TABLE 3. Replacement of adult losses through reproduction in carrion crow populations with different productivity and adult mortality rates. Juvenile mortality is assumed as constant from time of fledging until sexual maturity (2 years old).

	Number of fledged young per breeding pair per season					
	1.0		2.0		2.5	
Number of pairs	50		50		50	
'N'	100		100		100	
Adult mortality	40 %	20 %	40 %	20 %	40 %	20 %
Replacement needed	40	20	40	20	40	20
Number of young/year	50		100		125	
1st year mortality	62.4 %		62.4 %		62.4 %	
2nd year mortality	50 %		50 %		50 %	
Number of 2 years old	9.4		18.8		23.5	

collection of data or in his calculations. Until more precise information of carrion crow mortality rates are available, we can only assume that BUSSE's calculations quoted above are more realistic, and adult carrion crows, particularly the territorial population, have a similarly high survival as that reported by ROWLEY (1971) for the Australian species and by PATTERSON (personal communication) for Scottish populations.

4. Discussion and conclusions

The question has been raised in the introduction whether recently reported upward trends in carrion crow population numbers are real or illusory. To provide a basis for discussion three working hypotheses were constructed, which by and large would include all major possibilities.

Hypothesis A maintains that reports of increasing crow numbers are the results of subjective judgments, and therefore the increase is illusory. With the recent introduction of corn and other crops vulnerable to crow predation, the presence of the birds may be more obvious to the Swiss farmer now than before, even if the populations are stable. Because of its nature this hypothesis is difficult to prove or disprove, and will not be discussed further. We can only assume, that under certain circumstances it may hold true.

Hypothesis B would recognize real changes in population numbers, based on recent increase in breeding densities. Such changes may follow alterations of the breeding and feeding habitats providing more favourable conditions for breeding pairs, usually in agricultural areas and around human settlements. The well known adaptability of corvid species to utilize new opportunities must also be taken into consideration.

Hypothesis C claims that real population increase has not taken place, and breeding densities are more or less the same as before. The observed increase may reflect concentrations of non-breeding population surplus, resulting from decreased mortality rates and/or population movements to favourable areas by non-breeders.

The best approach to find an answer to these possibilities is, to examine what took place in the study population. As a starting point it should be emphasized, that concentrations of the carrion crows in the Wauwilermoos area is not a new phenomenon. According to local farmers the small wood of Chalpecherwald has

been a traditional roost for the birds for over a hundred years, even before the recent drainage of marshes to increase the area under cultivation. This must be taken as evidence for the history of a social group of population surplus in the region, as territorial pairs use the communal roost only occasionally, and chiefly during the winter. Such social groups are frequent among corvid species, and are very characteristic of the carrion crow (CHARLES unpublished manuscript, KALCHREUTER 1971, ROWLEY 1972, TENOVUO 1963, WITTENBERG 1968, YAMAGISHI 1962). In comparison with conditions in other countries, and even inside Switzerland, neither the size of the breeding populations nor the number of non-breeding surplus seems to be very high. There was a slight difference between the two study areas, the density of breeding pairs being higher in the woodland region among the hills. In the absence of previous records and of any evidence to the contrary, it can be safely concluded that the carrion crow population in the region has been relatively stable during the recent years.

If we completely disregard the existence of population movements between various areas, then the basis of a stable population size is, that the recruitment of new members through reproduction of the local pairs equals the yearly annual mortality among the breeders. As it has been shown in Section 3.4. the breeding population of Wauwilermoos falls short of that goal very drastically, and then the existence of a non-breeding surplus population still remains without explanation. Interestingly, other authors described simular situations in Germany, Finland and Britain, based on the given mortality rates and productivity figures. Even more interesting is, that carrion crow populations still do exist in those countries as well, and show no signs of coming to extinction. Two basic questions present themselves, firstly, what is the cause of low breeding success, and secondly, where is the sustaining balance coming from.

The answer to the first question is complex. In the present study as well as in Germany and Britain intrapopulation social interference where large groups are present was evident. Predation and nest competition with other species may also be a serious problem. But in Wauwilermoos as well as in Britain and Germany human interference was also considerable. The nearly 80—90 % nesting failures reported by WITTENBERG (1968) may be extreme, although a similar failure rate occurred in Wauwilermoos in 1974. When looking for a common denominator to explain the underlying causes of this rate of nest destruction, we come to the conclusion that in all these areas crows came into direct competition with human interest. All these studies were conducted in areas of high crow concentrations, in agricultural districts and around human settlements. Even in Finland, where TENOVUO (1963) described high incidence of nesting failures, the cause was nest destruction by hunters. There crows were effective predators on duck nests and nestlings, inviting reprisals.

This consideration at the end of the 1973 breeding season promoted the idea, that previous crow studies, including the present one, are strongly biased by focusing only on areas where crows are obvious by their numbers and occasional damage causing. But areas where these two factors are absent, where conflict with human interests is minimal or non existent, would have relatively undisturbed breeding populations of crows which could produce young not only to satisfy needs of the local population, but also to provide a relatively steady flow of emigrants into areas of low breeding success. If proved true, this explanation would answer the second question as well.

Where are such areas in Switzerland? The species' ecological range extends far beyond the normal 'study zone' of agricultural districts. They are tied to woodlands because of their nesting and roosting habits, and inhabit practically all regions of the country where these needs are satisfied and where open areas provide feeding grounds as well. Thus the forest covered hills, especially where the woods are broken up by openings, hill pastures, orchards and small farms, small valleys with meadows and other fields, etc. seem ideal to support breeding populations of the species. Such areas occupy the major part of the country, save the industrial zones and high elevations in the Alps. It was with this in mind that the study was extended into the neighbouring hills in 1974, searching for evidence to support the hypothetical explanation presented above.

When discussing the results it must be clear, that the entire study took only two summer and one winter seasons, far too short for final conclusions. Distinction should be made between factual and circumstantial evidence, and mere speculation. The factual evidence can be presented briefly. The density of the woodland breeding population was higher than that of the valley population with intensive agriculture. However, the two populations were distinct not only quantitatively, but qualitatively as well. While the large groups of social non-breeders were characteristic of the broadly open cultivated areas, they were almost completely absent from the hills. The only exception occurred at places where agricultural areas on the hills were continuous with that of the valley and covered a relatively large acreage. Thus the resident crow populations were almost entirely composed of territorial pairs and small family groups, where young stayed for a longer time with their parents.

When considering breeding success and productivity of the populations, the difference is even more spectacular and convincing. The number of young produced by breeding pairs was far too low in both years in the Wauwilermoos area to sustain the populations beyond a few years time, and the reports from other authors indicate, that the phenomenon was not just local and exceptional. No matter what the survival rate of the adult population was, extinction would be inevitable. The high breeding success of woodland pairs is a sharp contrast to this, where practically all territories had fledged young, as proof of the absence of human persecution. Assuming a high 75 to 85 % adult survival rate in the hills and woodland districts of Switzerland, the number of young surviving to recruitement age would be enough both to satisfy local needs and also produce an excess ready to emigrate into low productivity areas. This assumption finds strong support in observations of high survival of territorial pairs in Wauwilermoos, meaning an equally high or perhaps even higher survival in the neighbouring hills, where the breeding population is undisturbed by human interference. As shown in Section 3.4., such high survival among older age groups was reported from Scotland and Australia, and for European crows by BUSSE as well (1969). Without such survival rates the existence of crows in the country would be impossible. Communication between the hills and the broad agricultural valley of Wauwilermoos was evident, as single birds, pairs and even groups were often observed flying in and out of the area. Further evidence of immigration is the increase in the number of social non-breeders in 1974 over numbers of the previous year, which could not be explained by the reproductive success of 1973.

So far the factual evidence on quantitative and qualitative aspects of the problem. As circumstantial evidence explaining the obvious difference between

the productivity of the two populations we may consider the human effort to destroy crow nests in the agricultural districts in addition to attempts at keeping them away from vulnerable crops. With the exception of some scaring devices in orchards during the cherry season, such efforts are absent from the hills and woodlands. The rest remains a plausible speculation in the knowledge of the social behaviour, feeding ecology and other aspects of carrion crow natural history, available from world literature. As quantitative proof has been presented on the existence of two different types of populations as far as productivity and the presence of large social groups are concerned, the speculation is restricted simply to explain the underlying causes of these differences.

The carrion crow is a highly social species. Although such assemblages may well have a secondary function serving as information centers in food searching, as claimed by WARD & ZAHAVI (1973), their origin in the species would have a different explanation. As hardly any individual reaches sexual maturity before the age of two, and young of the previous year are expelled from the territories of their parents during the pre-breeding and the reproductive seasons, there is a considerable population of yearlings to form a nucleus of social gatherings. Such gatherings face different problems within agricultural districts and in the woodland hills. In the latter small openings, meadows and pastures, orchards, etc. can easily house territories and provide the young with sufficient food resources in late spring and early summer, but they can not support large groups that often grow to several hundred individuals. Furthermore, in the absence of large social groups the resident territorial pairs are more efficient in fighting off intruders during intense territorially active periods (TOMPA 1964), while in the broad and open agricultural areas such groups can easily shift from field to field opportunistically and also outnumber resisting territorial birds. Small groups still encountered in woodland areas are most of the time family groups, which may include even young from previous years prior to their reaching sexual maturity and becoming territorially active themselves (WITTENBERG personal communication).

Such family groups would break up in the hills during spring territorialism, when young of the previous year(s) are forced out from the territories. As large groups can not build up there they move into the valleys or wherever conditions permit the build-up of these gatherings, generally the agricultural areas. There they not only escape from the pressure of territorial pairs, but also have easy access to food and derive other benefits such as protection, from being in a group. Such 'immigration' need not be permanent, as after the breeding season they may return to the hills and join their parents again on their territories. The significant drop in the number of social birds by June and the observed movements to the hills by small groups and single birds strongly indicate this trend. They may return again to the valleys to the social groups when food and cover conditions worsen during the winters, and such opportunistic movements may considerably increase survival rates by making the immature population choose the best conditions available to them in the various seasons, both socially and foodwise. Stabilization of these movements would come at sexual maturation, or when they exhibit signs of territorial behaviour. If no vacant territories are available to them in the hills through the death within the adult breeding population, they are forced to emigrate on a permanent basis. Unless they find immediately a territory in a new locality, they would join the social groups where they may even form pairs, and stay within the structure until they perish or

eventually succeed to establish themselves within the local breeding population. Their previous movements as immatures act as conditioning to certain group areas, more or less predetermining the area of final settling.

As population densities are evidently higher in woodland areas unless they are unbroken forests, than in areas of intensive agriculture, and as such areas are far more characteristic to Switzerland than cultivated land, it is easy to see how a constant yearly immigration of population surplus from the hills not only compensates for the low productivity of the valley populations where social flocks are present, but also give an acceptable explanation to the existence of such groups. This shifting of the non-breeding population has both a positive and a negative feedback to the system. Breeding populations in the hills being freed of the surplus can maintain high productivity annually. The valley populations at the same time are sufferring from the presence of the social groups fed from the hills, with low productivity figures. To this the human interference invited by the presence of the social groups will be added. Although such negative feedback has similarities to the regulatory mechanism outlined by WYNNE-EDWARDS (1962), it contains decisive elements contributing to it from the outside in form of human action.

The situation, unless disproved by continued research in the hills, strongly supports *Hypothesis C* as outlined above, explaining the apparent population increases of the carrion crows by movements of non-breeding surplus. This does not exclude the possibility that under certain local conditions environmental changes has increased the number of breeders by improvements of the breeding habitat. However, drastic population changes cannot be expected from *Hypothesis B*, and at least in the present study population densities of breeding pairs in the valley and in the hills do not indicate increased territorial populations in the former regions.

As a final conclusion the existence of two qualitatively and quantitatively different populations should be emphasized under conditions prevailing in Switzerland, as proven by the absence or presence of social groups and by the drastically different productivity figures. A higher survival among adult birds may also be expected in woodland areas where populations are free both from human interference and intrapopulation social pressure, but this must be proved by an extensive and intensive banding, release and recovery program. The well known social behaviour, feeding habits and other aspects of the ecology of crows help to build up a complex picture that explains the proved differences in the numbers and the structures of these populations.

SUMMARY

1. A field study was carried out during the 1973 and 1974 summers and the intervening winter to determine the causes of an apparent increase in population numbers of the carrion crow in Switzerland. The study area included a valley under intensive cultivation close to Sursee in Luzern kanton, where large numbers of crows are normally present. In the second year the investigation was extended to the neighbouring woodland areas as well. As banding programs could not be carried out for technical reasons, data were collected through regular and almost daily observations of the populations.

2. Population densities of breeding pairs in the valley and in the woodlands were 3.0 and 3.7 per km^2 respectively, and there were indications of relative stability of numbers.

3. In the agricultural valley large groups of social non-breeders were evident, although their numbers showed seasonal fluctuations, indicating not only recruitment through reproduction, but also an influx of immigrants from the surrounding woodland hills. In the woodland area social groups were absent. The social groups were evidently composed of immature birds as well as older age groups, the latter ready to reproduce. Their presence within the groups is explained by lack of space within the territorial breeding population.

4. Breeding success of the valley population was extremely low both seasons, 1.0 and 0.47 fledged young per breeding pair. The nesting failure rate of breeding pairs in 1973 and 1974 was 0.67 and 0.8 respectively. The low productivity is explained both by the social pressure by the non-breeders upon the breeding population, and also by strong human interference with breeding in intensive agricultural areas. This situation has similarities with the low breeding success of British, Finnish and German crow populations which had been studied in regions where crows and human interests are in conflict. By contrast the woodland population in 1974 had a failure rate of only 0.13, and a minimum of 2.4 young were fledged per participating pair, drastically higher than in the valley population.

5. The observed productivity figures together with the assumed mortality rates from other crow populations cannot explain how these populations are sustained, as they should decline to extinction within a few years time. It is argued that only an influx of immigrants from high productivity areas can explain the existence of the valley population. The obtained productivity figures from the valley and the woodland hills, the presence and absence of social groups in the respective areas and the observed movements of birds between them are taken as factual evidence to support the argument. The difference is explained by the presence of both social pressure and human persecution in the agricultural areas depressing breeding success, while the absence of social groups from the woodland hills is presumably the result of both the pressure by territorial birds upon the non-breeding surplus and also by the lack of space to support large gatherings. This differences have both a positive and a negative feedback to the system by maintaining high productivity in woodlands and by repressing it in agricultural areas or in regions where crows and man compete directly.

6. It is concluded that the apparent increase in crow population numbers presumably does not mean an increase in breeding densities, but reflects the influx of birds from the high productivity areas into agricultural regions and to the surroundings of human settlements, where large groups can build up and winter survival may be increased by food resources supplied through man-made alterations of the environment.

ZUSAMMENFASSUNG

Zum Rabenkrähen-Problem in der Schweiz
1. Teil: Allgemeine Einführung und Populationsprobleme

1. Im Zusammenhang mit dem ausgedehnteren Maisanbau wurden in letzter Zeit vermehrt Klagen über eine Zunahme der Rabenkrähe und der von ihr verursachten Schäden an den Kulturen laut. Im vorliegenden ersten Teil dieser Arbeit wird die Ökologie und Populationsdynamik der Rabenkrähe unter den spezifischen Verhältnissen im Schweizerischen Mittelland untersucht um zu prüfen, ob die Art wirklich zugenommen hat. Im später folgenden zweiten Teil soll versucht werden, ihre Bedeutung für die Landwirtschaft zu beurteilen.

2. Als *Untersuchungsgebiet* wurde eine rund 12 km² grosse Fläche im Wauwilermoos (westlich von Sursee LU) gewählt. Der flache zentrale Teil ist intensiv bewirtschaftetes Gebiet mit einigen Baum- und Buschreihen; darum herum liegen vereinzelte Bauernhöfe mit kleinen Obstgärten. Ein Drittel der Fläche ist Grasland, daneben wird viel Mais sowie etwas Kartoffeln und Gemüse angebaut. In der Brutzeit 1974 wurde das Untersuchungsgebiet auf das südöstlich angrenzende Hügelgebiet ausgedehnt (6.5 km²). Dort herrschen — neben dem etwa die halbe Fläche einnehmenden Mischwald — Wiesland und Obstgärten vor. Mais fehlt fast ganz.

3. *Methode:* Da nicht genügend Krähen beringt werden konnten, wurde das ganze Untersuchungsgebiet während der Brutzeiten fast jeden Morgen und Nachmittag began-

gen, um möglichst alle anwesenden Krähen zu erfassen. Im Herbst und Winter wurden pro Woche zwei bis drei Zählungen durchgeführt.

4. *Brutpopulation.* In den beiden Jahren waren im Wauwilermoos 36 Brutreviere besetzt (3 Paare/km², was für das Mittelland relativ wenig ist). In den Obstbaum-Arealen lagen die Reviere dicht beisammen, in Gebieten mit weniger Bäumen wurden auch die Reviere seltener (Abb. 1, 2). 1973 betrug der mittlere Nestabstand 353 m. In beiden Jahren wurden zwei Reviere von je drei Krähen verteidigt. Im Hügelgebiet war der Brutbestand mit 3.7—4.1 Paaren/km² deutlich höher.

5. *Nichtbrüter.* In der Ebene kam zu den Brutpaaren noch eine wechselnde Zahl Nichtbrüter, die in lockeren Schwärmen leben. 1973 lag das Verhältnis Brüter : Nichtbrüter bei 1 : 1, 1974 bei 1 : 3. Während der Brutzeit nahm die Zahl der Nichtbrüter in beiden Jahren vorübergehend zu (Abb. 4). Im Herbst und Winter schwankte der Schwarmvögelbestand in Abhängigkeit von der Witterung. Bei sehr schlechtem Wetter schlossen sich auch Brutpaare aus den Hügeln den Schwärmen an. Da keine Krähen beringt waren, liess sich die Alters- und Geschlechtszusammensetzung in den Schwärmen nicht genau angeben. Verschiedene Anzeichen lassen aber einen hohen Anteil geschlechtsreifer, zum Teil verpaarter Individuen annehmen, die kein Brutrevier besetzen oder aus anderen Gründen nicht zur Fortpflanzung schreiten konnten. Ins Hügelgebiet kamen Schwarmvögel nur zum Nächtigen.

6. *Bruterfolg.* 1973 wurden im Wauwilermoos 12 Bruten genauer kontrolliert (Tab. 2). Die mittlere Gelegegrösse betrug 4.1 Eier (n = 9). In der zweiten Hälfte der Nestlingszeit waren noch durchschnittlich 3.4 Junge im Nest (ohne Totalverluste gerechnet). Bezogen auf alle untersuchten Nester flogen aber nur 1.0 Junge pro Paar aus. In der ganzen Population der Ebene kamen nur in 13 der 36 Nester Junge hoch (Abb. 1), ebenfalls rund ein Junges pro Paar. 1974 war der Bruterfolg mit 0.47 Jungen pro Brutpaar noch niedriger; in nur 6 der 36 Nester wurden überhaupt Junge flügge (Abb. 2). Ein Teil der Brutverluste ist sicher auf die Schwarmvögel zurückzuführen (intraspezifischer Nestraub), da fast alle Brutversuche in der Nähe der Schwarmareale missglückten. Mindestens zwei Nester wurden während der Brutzeit von Elstern *Pica pica* zerstört und zwei von Mäusebussarden *Buteo buteo* geplündert. Der grösste Teil der Brutverluste war jedoch auf den Menschen zurückzuführen. Eine solche Situation ist typisch für Gegenden, in denen die Krähen mit menschlichen Interessen in Konflikt geraten. In den waldigen Hügelgebieten, wo das nicht der Fall ist, hatten 1974 nämlich mindestens 21 von 24 Paaren Junge (2.4 pro Paar der ganzen Population).

7. *Mortalität und Populationsdynamik.* Aus der Zahl der in beiden Jahren vom gleichen Paar besetzten Revieren wird die Überlebensrate der Brutpopulation auf mindestens 0.78 geschätzt. Von 6 farbberingten Jungen konnten nach einem Jahr noch 4 beobachtet werden; wegen der relativ guten Wetterverhältnisse im Winter 1973/74 schien auch die Mortalität der nicht beringten Jungen recht niedrig gewesen zu sein, liess sich jedoch nicht genauer abschätzen. In Anbetracht der in der Literatur angegebenen Mortalitätsraten (0.62 für das erste und 0.5 für das zweite Lebensjahr) müsste eine Population mit weniger als 2.5 Jungen pro Paar und einer Adultmortalität über 0.2 in wenigen Jahren aussterben.

8. Die Population im Wauwilermoos kann sich demnach gar nicht selbst erhalten, so dass eine Zunahme der Krähen durch einen angewachsenen Brutbestand nicht anzunehmen ist. Zudem liegt die Bestandesdichte auch heute deutlich unter dem schweizerischen Durchschnitt. Da der Schlafplatz am Rand des Untersuchungsgebietes schon seit mehr als hundert Jahren bestehen soll, dürften auch früher schon Schwarmvögel im Gebiet gewesen sein. Ein grosser Teil dieser Schwarmvögel muss aus Gegenden mit höherem Bruterfolg eingewandert sein. Solche Gebiete sind vor allem waldreiche Hügellandschaften mit Wiesen, Weiden, Obstbäumen usw., die den grösseren Teil des von der Rabenkrähe in der Schweiz bewohnten Geländes ausmachen. Da die Krähen dort weit weniger mit menschlichen Interessen in Konflikt kommen, ist auch der Bruterfolg so hoch, dass nicht nur die eigenen Verluste ersetzt werden können, sondern auch ein Überschuss an Jungvögel in Gebiete mit zu niedrigem Bruterfolg abwandern kann.

9. Spätestens im Frühjahr werden die Jungvögel aus den Revieren der Eltern vertrieben und schliessen sich dann, da sie ja noch nicht geschlechtsreif sind, zu Schwärmen zusammen. Hügelgebiete ohne grosse, offene Flächen bieten für grössere derartige Schwärme nicht genug Nahrung, andererseits können kleinere Gruppen von den ansässi-

gen Paaren leicht vertrieben werden. In den Ebenen dagegen können sich diese Nichtbrüter dank der guten Nahrungsbedingungen und ihrer Überzahl leicht gegenüber den Brutpaaren behaupten. Wenn nach der Brutzeit die Reviere nicht mehr stark verteidigt werden, kehrt ein Teil der Schwarmvögel wieder in die Hügelgebiete zurück. Finden geschlechtsreife Schwarmvögel dann ein freies Revier, bleiben sie dort, andernfalls müssen sie sich während der Brutzeit wieder den Schwärmen anschliessen.

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