

Barn owl *Tyto alba*: Dynamic and breeding success of a population in Lower Saxony, Germany.

by Ernst Kniprath

Contents

1. Introduction.....	2
2. Material and methods.....	2
3. Results.....	3
3.1 Breeding sites.....	3
3.2 Breeding seasons.....	5
3.3 Broods.....	7
3.3.1 Second broods.....	8
3.4 Breeders.....	8
3.4.1 Origin of breeders.....	9
3.4.2 Abode of the breeders.....	12
3.4.3 Pairs.....	13
3.4.3.1 Properties of pairs.....	13
3.4.3.2 Mate fidelity.....	13
3.4.3.3 New pairings after loss of mate.....	13
3.5 Breeding success / Quality.....	14
3.5.1 Quality of breeding sites.....	14
3.5.2 Quality of breeders.....	14
3.5.2.1 Breeding success and age.....	15
3.5.2.2 Breeding success and mate fidelity.....	17
3.5.2.3 Breeding success and laying date.....	17
3.5.3 Quality of pairs.....	18
3.5.4 Success of second broods.....	20
3.6 Alterations in the population.....	20
3.6.1 Dynamics.....	20
3.6.2 Mortality.....	21
3.6.3 Dispersion.....	22
3.6.4 Productivity.....	22
3.6.5 Balance.....	22
4. Discussion.....	23
4.1 Breeding sites.....	23
4.1.1 Choosing a breeding site.....	23
4.2 Quality of years.....	24
4.3 The breeders.....	24
4.3.1 Site fidelity of the breeders.....	24
4.3.2 Age of the breeders.....	24
4.3.3 Mate choice.....	25
4.3.4 Mortality.....	26
4.4 Density dependence.....	26
5. Literatur.....	28

1. Introduction

Depending on food supply (predominantly voles) the numbers of barn owls generally vary considerably (GLUTZ VON BLOTZHEIM & BAUER 1994). Though the species is called sedentary it is uncertain which movements are performed from year to year by the adult birds. Consequent monitoring of the breeding population should lead to a better understanding of this and of some more questions concerning population biology as well as partnerships and the dependences of breeding success. Even if the material presented does not belong to the greater data collections the results seemed worth to be communicated. For Germany it is the first study of an exclusively nest box population with a technically conditioned very high catching rate of adult birds.

2. Material and methods

The eastern part of the county Celle (including the "Samtgemeinde" Lachendorf, a northern part

of the Samtgemeinde Flotwedel, and the southern part of the Samtgemeinde Eschede) contains parts of the "Südheide" (southern heath) and of the Aller-low-land with its centre at about 10,30E, 52,63N, 40 – 70 m above sea level. Here on an area of about 220 km² between 1967 and 1979 nest boxes for barn owls were installed predominantly in rural buildings (ALTMÜLLER 1981). At the end of these activities the total number of boxes had reached 22 in 18 regularly controlled agglomerations (of 26) (Fig. 1). This means a density of 10 controlled boxes / 100 km² or 1,2 boxes / village with boxes. Some more boxes in the surroundings were not controlled regularly. The data collected there (concerning 19 controlled broods) were considered in this study only exceptionally (e.g. for the birds origins and whereabouts of the breeders). The boxes were fastened to the inner side of the exterior walls of the buildings with entrance from the outside of the buildings.

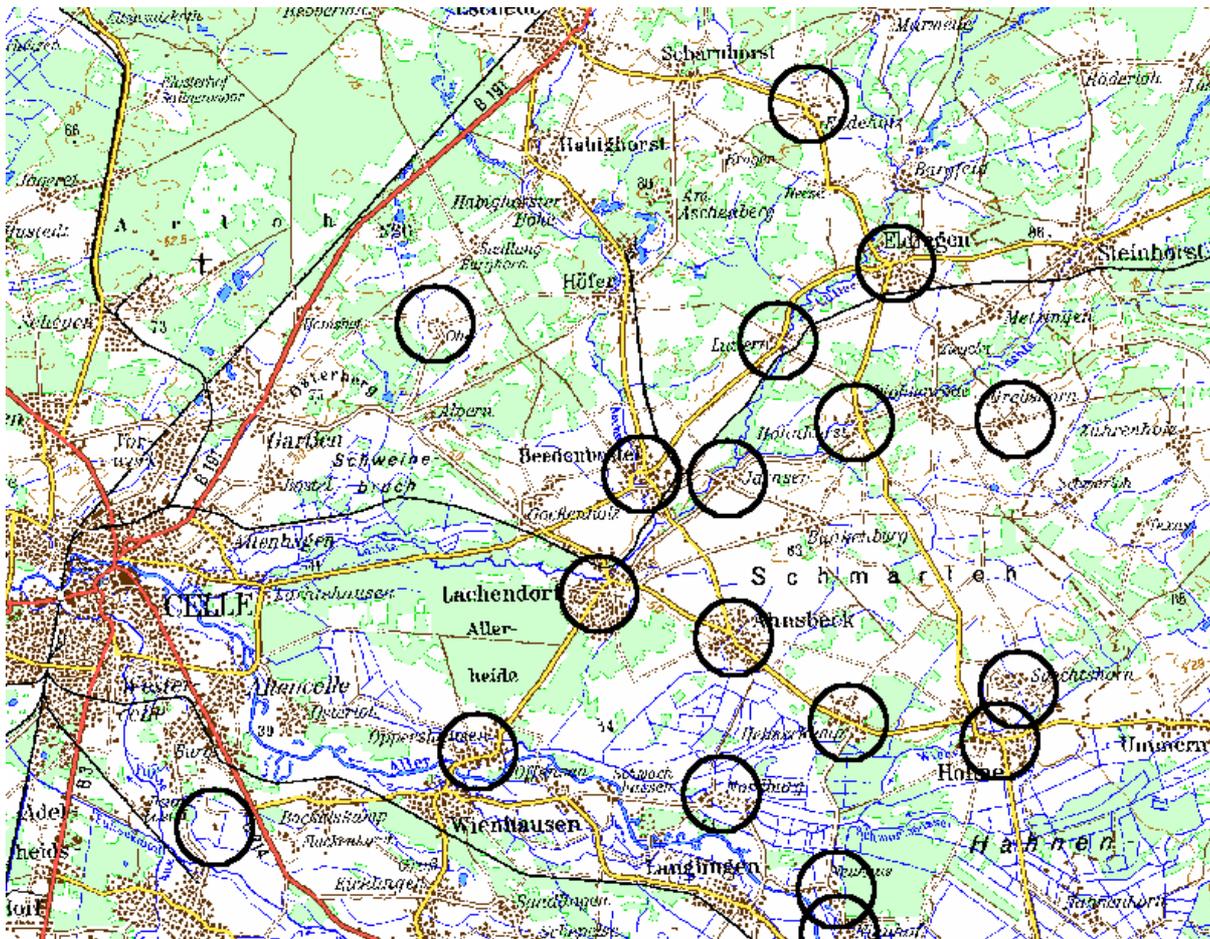


Fig. 1: The study area and the distribution of villages with nest boxes

From 1972 to 1992 the nest boxes were controlled annually, the adult birds were caught (see ALTMÜLLER 1980) and ringed or controlled (altogether 83 ♀ and 64 ♂) and the young of 151 broods ringed as well. Of the theoretically 304 parent birds of 152 broods 242 were controlled (=79,6%; ♂ : 116 =76,3 %; ♀: 126=82,9%). Broods outside boxes were found only twice (in a dovecot). Additional broods cannot be excluded as in 6 villages boxes were not known. Further more these villages were not controlled for free broods.

For protection causes controls possibly were not performed before well developed pulli could be expected.

The following analyses – if not noted otherwise – only use obvious first broods. The success values (numbers of eggs, hatched and fledged young) partly were registered only indirectly (for the late data of controls) but mostly determined. The numbers of eggs mean a minimum as in a greater number of broods the egg number was equalled the number of young found at the controls. This also is true for the number of hatchlings. The number of fledglings was

equalled the number of young ringed. So it is a maximum number as sometimes young “fall” out of the boxes and can be preyed by some predator without being realized by the student. Carcasses found later when cleaning the boxes diminished the number of fledglings. The numbers (N) in the tables and figures partly differ as occasionally missing basic numbers were taken into consideration. Diagrams and regression lines were produced with Microsoft EXCEL.

All results exclusively base on ringed (mostly with rings of the “Vogelwarte Helgoland”) and controlled birds. I am grateful to Dr. R. Altmüller and H. Könecke for kindly rendering me the original data of their ringing and controlling activities.

3. Results

3.1 Breeding sites

In 17 of the 18 villages with boxes (94,4%) and within 21 of the 22 nest boxes (95,5%) actually broods took place. The distribution of the broods in the study area is given in Fig. 2.

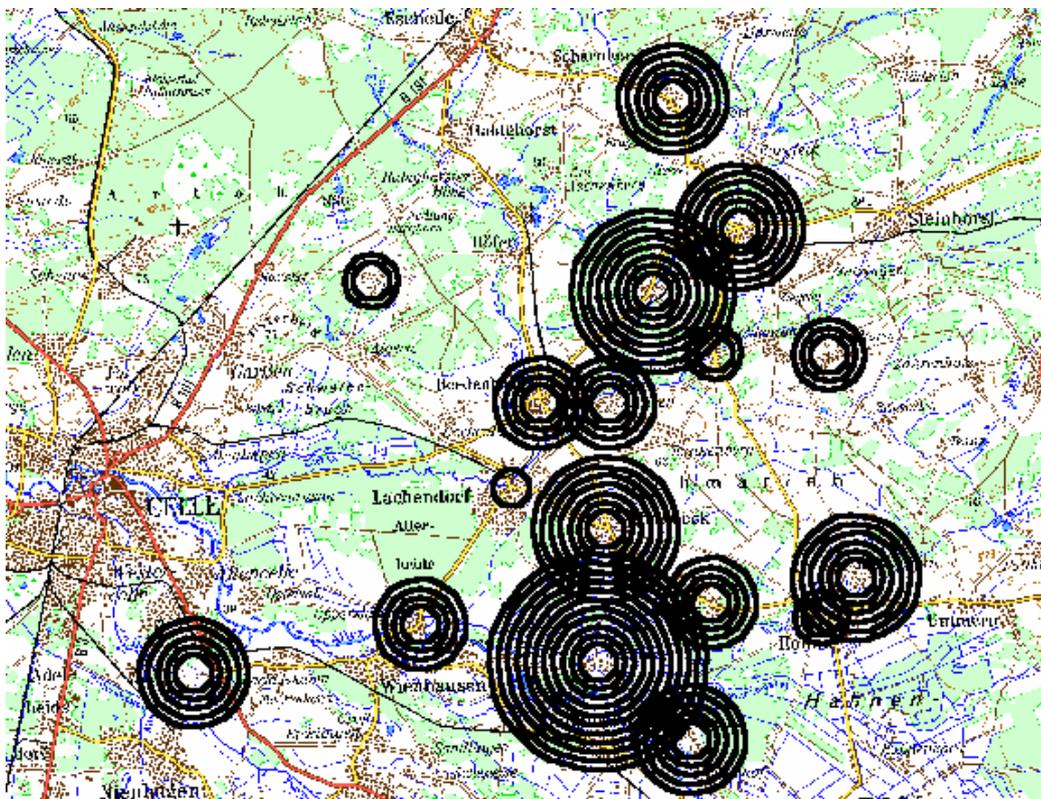


Fig. 2: The distribution of the broods in the study area: each circle counts for two broods (data from table 1)

It is striking how differently often broods were performed at the different sites. Table 1 gives the rank of the breeding sites by counting the number of (first) broods. The ranks are taken as a preliminary measure of the quality of the respective site. In the villages with rank 1 and 2 23,7% of the broods took place, in the worst years even >50%. The high popularity of these for the barn owls obviously is persisting.

Table 1: Rank list of the villages by numbers of broods

Village name	Number of broods	rank
Nordburg	21	1
Luttern	15	2
Ahnsbeck	13	3
Neuhaus	12	4
Eldingen	11	5
Spechtshorn	11	5
Endeholz	10	6
Gr. Ottenhaus	9	7
Beedenbostel	9	7
Jarnsen	9	7
Oppershausen	7	8
Helmerkamp	7	8
Grebshorn	5	9
Hohne	4	10
Hohnhorst	4	10
Ohe	4	10
Lachendorf	1	11

To examine wherein this popularity manifests, the staying time of the single breeder at the breeding site once chosen, and the popularity of each place for newcomers, and as moving destiny was determined. Nineteen breeding pairs were found in two successive years. Seventeen of them stayed at the site, two moved. At both of these moves a higher ranked site was chosen.

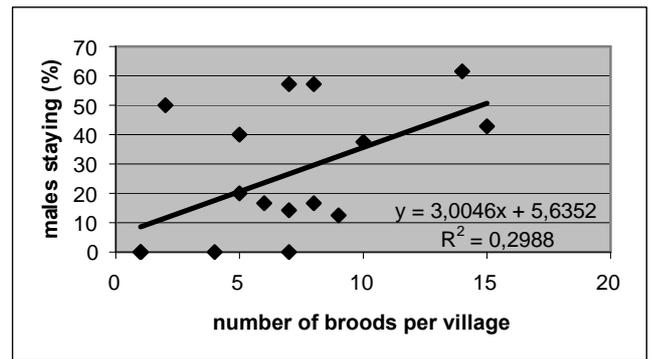


Fig. 3: The portion of ♂ staying from one breeding season to the next one in dependence of the number of broods at the respective site; N=33 (see tab. 1)

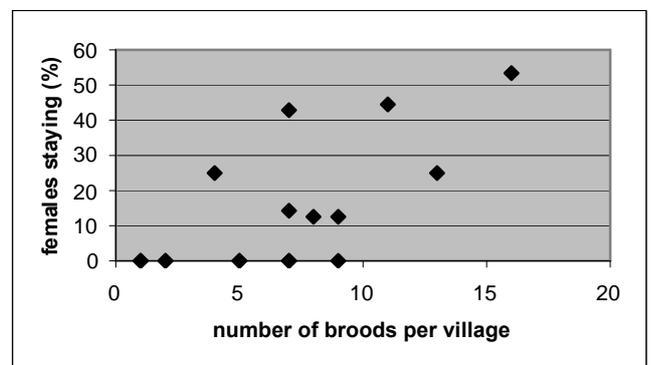


Fig. 4: The proportion of ♀ staying from one breeding season to the next in dependence of the number of broods at the respective site; N=38 (see tab. 1)

The figures 3 and 4 show that those breeding sites – with considerable deviations – that generally are preferred for breeding also show a greater proportion of staying breeders. Consequently the staying time of the breeders at these sites is longer (Figs. 5 & 6): ♂ like ♀ stay longer at sites of higher rank where in ♂ this correlation is more obvious.

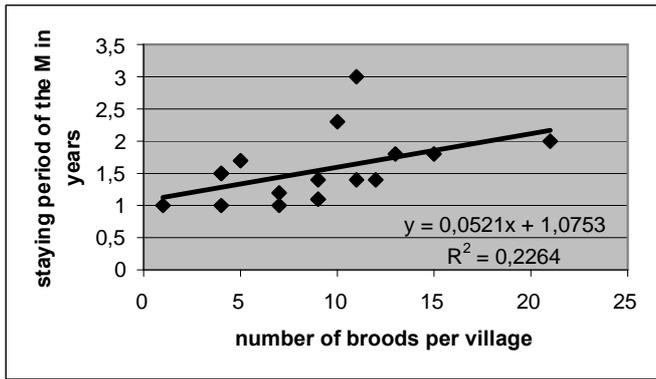


Fig. 5: Correlation between total number of broods in a site and the staying period of the ♂ there; N=18 (see tab. 1)

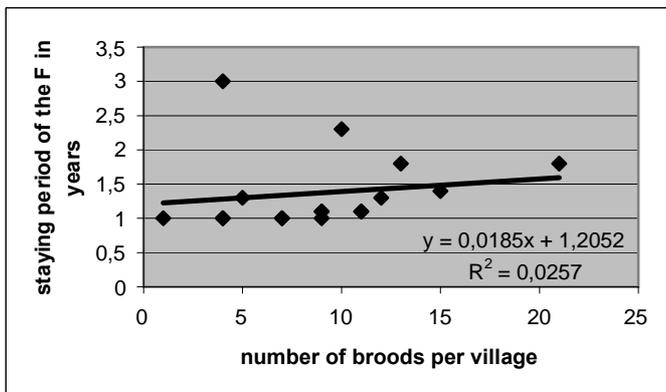


Fig. 6: Correlation between total number of broods in a site and the staying period of the ♀ there; N=23 (see tab. 1)

If the breeding site (within the study area) is changed the following image results: 14 moves of ♂ and 13 of ♀ were at disposition. ♂ moving in the study area preferred boxes of higher rank (after Table 1) (Fig. 7). As the exact moment of the moves (between the end of brood A and the beginning of brood B) in each case is unknown we could not examine whether a better breeding site was available at all.

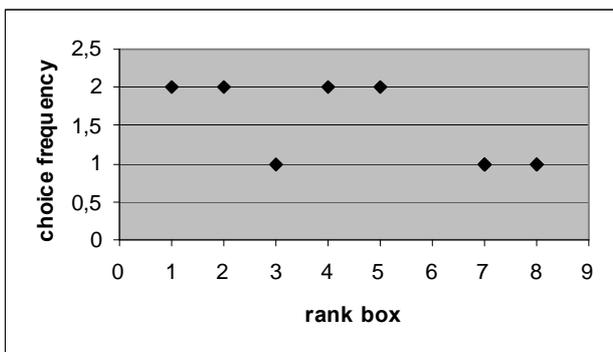


Fig. 7: The frequency with which a box was chosen by moving ♂ (within the study area) depending on the rank of the box; N=14

Furthermore we examined whether the quality of a box is already recognizable for arriving immigrants.

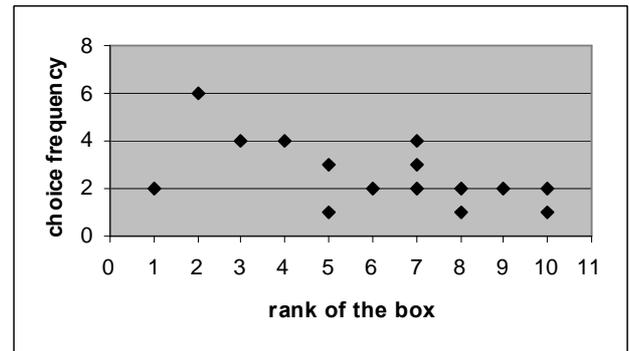


Fig. 8: Frequency with which a box was chosen by moved ♂ (from outside the study area) depending on the rank of the box; N=39

Fifteen of the boxes used at all during the study period were used by immigrant ♂. Fig. 8 shows that these ♂ of course can realize the quality of a box. They prefer boxes of higher ranks. In particular: In 20 (of 37 possible) cases of new settlement the box actually chosen was not occupied the preceding year. Four times it was one of the two top rank boxes. In 13 cases there was a pre-owner, in 5 of these cases the latter remained unknown, in 5 additional ones he was known indeed but controlled no more. Three more left the box (twice a top rank box) and bred elsewhere. In these three cases the pre-owner could have been chased out by the immigrant. In the 31 cases in which the immigrants did not succeed to occupy one of the top ranked boxes 18 of the latter had been occupied the year before and also 23 in the respective breeding period by a different ♂.

Recruits of the local population (♂, N=11) which in fact could know the quality of the boxes settled without any recognizable preference by rank. Eight of the boxes occupied by them had been free in the preceding season, in one of them there bred an unknown and in the two remaining ones a ♂ which was not controlled later. So we may deduce that recruits settle in any free boxes.

3.2 Breeding seasons

Mostly depending on prey supply the numbers of barn owls and those of their breeding success differ considerably from one season to the next (e.g. TAYLOR 1994). Scattering around a mean value (of all broods, as far as data are known) of

3,61 fledglings the success values of our population vary as well (Tab.2).

Table 2: Number of broods and mean values of clutch size, hatching and fledging numbers (second broods included) per study year.

year	broods	eggs	hatchlings	fledglings
1972	4	4,75	4,75	3,00
1973	2	5,00	1,50	1,50
1974	3	5,33	5,33	5,33
1975	7	5,57	4,57	3,29
1976	2	5,00	2,50	2,50
1977	4	7,25	5,50	4,50
1978	15	5,47	5,27	4,80
1979	3	3,67	3,00	3,00
1980	4	4,50	4,50	3,50
1981	9	5,11	5,00	4,89
1982	10	3,10	3,00	2,90
1983	10	4,40	3,20	3,10
1984	16	4,13	2,94	2,63
1985	6	3,50	3,50	3,33
1986	10	4,50	4,20	3,70
1987	3	3,00	3,00	3,00
1988	3	4,67	4,67	4,00
1989	5	6,00	5,00	4,60
1990	12	5,33	3,67	3,50
1991	12	4,33	4,17	4,08
1992	12	4,00	3,25	3,25

So the number of broods per year is a first measure for the quality of a year. Nevertheless there is only a weak correlation between the number of broods and that of the fledglings of the respective year. Being probably of significance whether a certain level of the breeding population was the result of an increase or a decrease we could perhaps deduce a better measure for the quality of a year from the alterations of the population numbers – independently of their real value. As expected figure 9 shows that the yearly alterations of the brood numbers scatter around the zero line. Indeed they do not exactly, but the regression line is above zero over all its length: The increase dominates. The negative trend of the line moreover demonstrates that the nest box campaign reached its optimum: Towards the end of the study the population obviously increased no more.

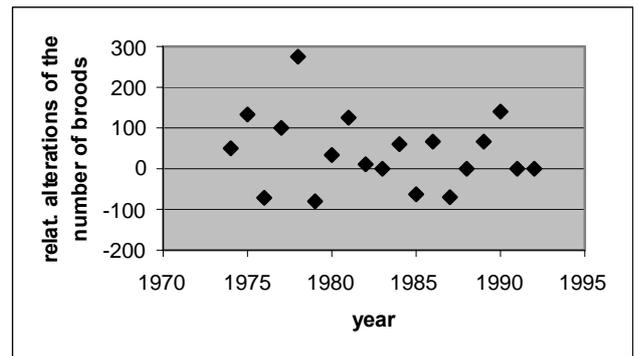


Fig. 9: Relative alterations of the number of broods against previous year

But also the alterations alone do not seem to be sufficient to demonstrate the quality of the years as in these figures it is not integrated at which level these alterations happened. As we don't have a measure for this level the years purely were ordered by impression (column "tendency" in table 3)."

Table 3: List of the developmental tendencies of the barn owl numbers from year to year and assignment of the latter ones to new categories. (see text)

tendency	category
downwards	5
considerably downwards	1
remaining low	4
slightly upwards	8
upwards	6
considerably upwards	7
increase on high level	3
remaining high	2

Starting with the mean values of clutch size of all years belonging to each tendency these latter ones were ordered by increasing values. The resulting ranks can be found in the column "category" in table 3. Then this category was associated with each year. The correlation in figure 10 shows that despite all scattering of the single values this classification seems to be valuable as quality measure. Using mean values of the numbers of hatchlings or fledglings instead of the clutch size only produced a higher scattering.

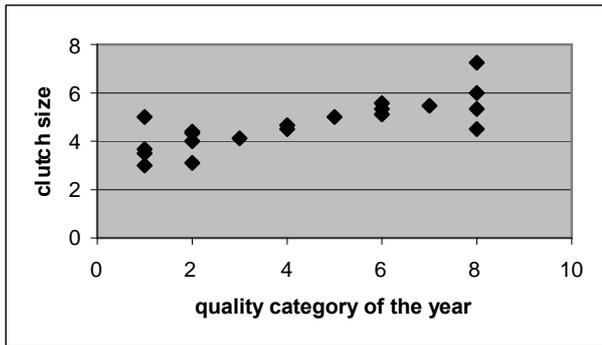


Fig. 10: Mean values of clutch size from table 2 ordered by category of the year (see tab. 3)

Furthermore we examined whether the age composition of the population and the egg laying dates altered from year to year. Figure 11 shows a correlation between the mean age of the ♂ and the number of broods in the respective year: In years with low brood numbers, i.e. in worse years, the ♂ on average are one year older than in very good ones. This counts as well for ♀. The use of rank numbers from table 3 instead of the number of broods obviously did not increase the correlation. For the age composition of the population see figure 16.

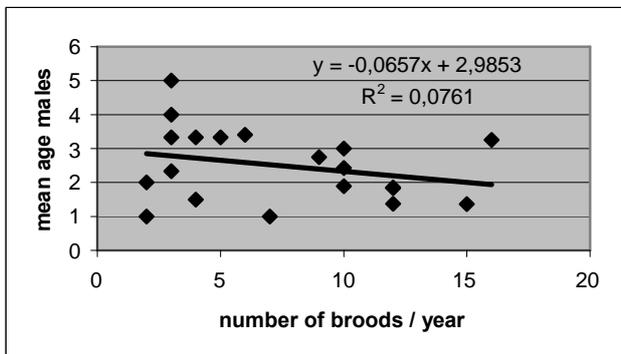


Fig. 11: Correlation of number of broods / year and mean age of ♂ (first broods only)

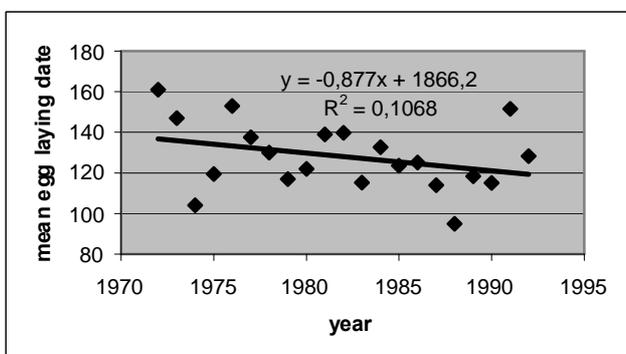


Fig. 12: Scattering of mean egg laying date of broods in the first half of the year (in days after beginning of the year); N=95

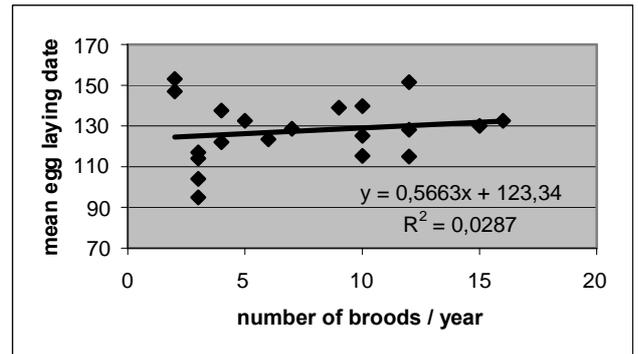


Fig. 13: Correlation of mean egg laying date (in days from beginning of the year) and number of broods / year (first broods only)

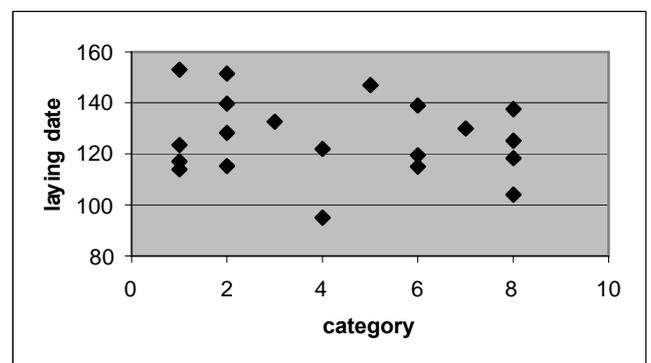


Fig. 14: Correlation of mean egg laying date (in days from beginning of the year) and category of quality (after table 3)

As figure 12 clarifies in the 20 years of study the owls have advanced the egg laying date for almost 20 days (used only broods of the first half of the year where laying dates are known). Additionally in figure 13 is shown that the egg laying date is later in good years than in worse ones. If we use for comparison the ranks of the years (after table 3) instead of the number of broods, an almost similar picture results (Fig. 14): With great scatterings the laying date is delayed with augmentation of the quality of a year.

3.3 Broods

Following with delay the increase of nest boxes the owl numbers increased too but discontinuously (Fig. 15). Altogether 152 broods were registered. Almost surely 124 of these were first broods for at least one ore both mates, four for at least one mate second broods. Though six of the first broods remained unsuccessful no replacement brood was observed. Probably there were some but due to the late control date (see material and methods) they were not identified as such.

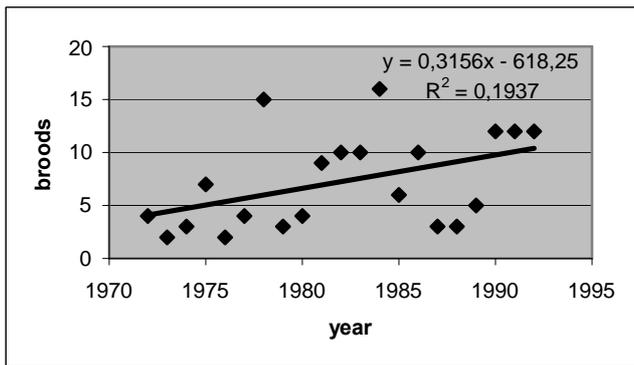


Fig. 15: Numbers of broods (first half of the year only)

3.3.1 Second broods

All over only five second broods were detected in the years 1974, 1980, 1986, 1988, and 1991 resp.. As can be seen in table 2 the years considered belonged to very different types. After a preceding decrease, 1974, 1980, and 1986 showed an increase, 1988 stagnation on a very low level, and 1991 stagnation of the broods on a very high level.

These second broods themselves belonged to three different types: Two of them (1986 and 1988) were second broods of a pair each, the belonging ♂ six and at least three years old, the ♀ at least two and five years old. The ♂ of the brood 1986 afterwards was not recorded again, the other one bread two more years (at least one of these with the known ♀). The ♀ concerned thereafter bread for five resp. four more years. These two second broods were realized each in the same box as the first one.

Two of these broods (1974, 1980) were divorce second broods, i.e. the ♀ deserted their first broods just before fledging and made a second brood with a new mate (for definitions see KNIPRATH & SEELER 2005). All birds involved had not been known before. The mates of the year 1974 and the ♀ of the year 1980 were no more seen later, the ♂ of the year 1980 later bread for four more years. These two divorce second broods were at distances of 8,1 resp. 4,0 km apart from the first breeding sites of the resp. ♀. The time intervals between the laying dates of the first and the resp. second broods were counted being 83 resp. 60 days. As normally about 90 days are needed for a brood until fledging these were overlapping broods (in German: Schachtelbruten) (for the first one see ALTMÜLLER 1976).

The fifth brood (1991) was the second one of that year of a ♂ not known the year before, but not with his mate of his first brood. The egg laying interval to the first brood of the ♂ only counted 74 days. As a normal brood needs about 90 days until fledging of the young, we here do have a case of bigyny.

Concerning this ♂ we know some more details: He was caught at his first brood together with a second ♀ known as breeding bird of the year before. There is no proof for any participation in the brood of this ♀. Perhaps she acted as helper. She was no more registered later. The ♂ made his second, the bigynic brood with a third ♀ hitherto unknown. She too was no more seen later.

3.4 Breeders

For 116 of the 152 broods the ♂ could be controlled and for 126 the ♀. Of the really participating 64 ♂ (several were multiple breeders) 18, and 15 of the 83 ♀ were known by their exact age. They had been ringed as nestlings.

The controlled ♂ amounted yearly 44 to 100%, mean 77,0%, the ♀ 50 to 100%, mean 83,1% (1972 not counted). The mean age of the breeders of known age summarized over all their broods was 2,3 years, SD 1,6 (♂), resp. 2,7 years, SD 2,0 (♀). The summarized age structure of the breeding population is shown in figure 16. As there were only 18 ♂ and 15 ♀ of exactly known age we looked for a method to judge the age of a greater part of the population. On their first brood recorded the 18 ♂ of exactly known age had a mean age of 1,33 years, the 15 ♀ of 1,4 years resp.. As both these numbers are clearly beyond 2 all immigrated birds were counted being yearlings. So the numerical basis was enlarged clearly. For some of the following analyses the breeders were grouped according to their age: yearlings, medium aged (2-3 y), and aged (>3 y). It became visible that the proportion of the ♀ is distinctly high in the yearlings and that of the ♂ in both other age groups.

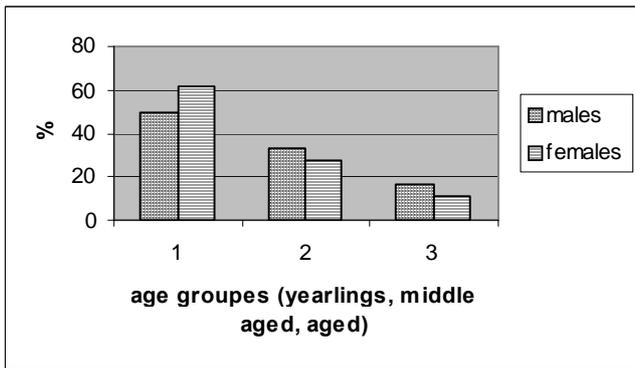


Fig. 16: Summarized age structure of the breeding population (yearlings, middle aged (2-3 years), and aged (>3 years)) 1973-1992

Eighteen ♂ known exactly by age were engaged in 31 broods (30 with known results, mean 1,7), 15 ♀ in 29 (28 with known result, mean 1,9). The all over numbers are: 64 known ♂ made 116 broods, mean 1,8, the 83 ♀ 126, mean 1,5. The figures 17 and 18 demonstrate the numbers of broods in which the breeders known by age took part depending on their age.

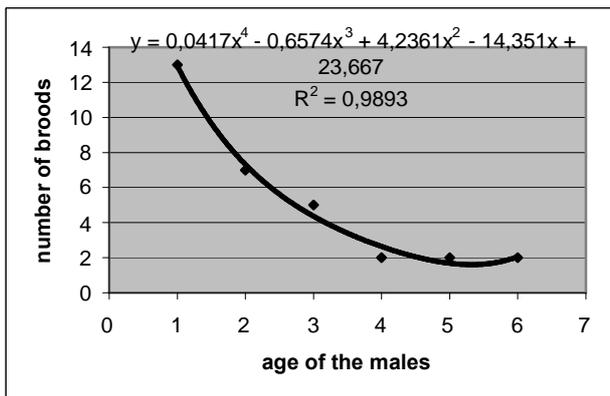


Fig. 17: Participation of the ♂ of known age in the broods; N=31

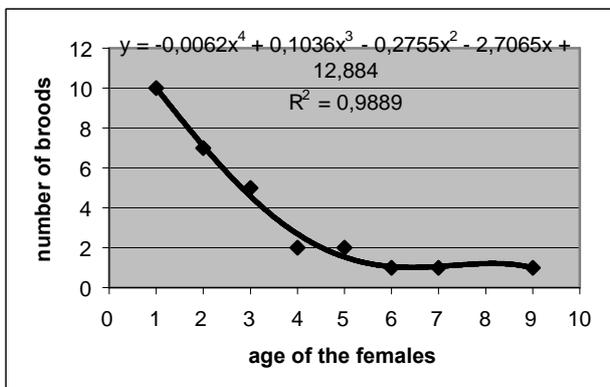


Fig. 18: Participation of the ♀ of known age in the broods; N=29

3.4.1 Origin of breeders

The breeding population of each single year is composed of three portions: recruits of the preceding years (known by age), the breeders of the preceding years staying in the study area (in part resident and in part moved), and the immigrants (in part known by age). The respective portions are summarized in table 4.

Table 4: Origin of the known breeders of all years

	♂	♀	sum
Immigrated, known by age	7	9	16
Immigrated, not known	10	8	18
Own breeders	47	36	83
Own recruits	8	5	13
sum	72	58	130

Twelve of the 16 immigrants known by age were yearlings (5♂, 7♀), the remaining ones at least two years old. Five of the own recruits (3♂, 2♀) were at least two years old. For these nine (4 immigrants and 5 own recruits) being older than one year I guess that they already had bred outside the study area before moving, or inside without being detected. But as there is no proof, they are not counted as immigrated breeders. Table 5 gives the composition of the own breeders by their moving behaviour. Herein the 15 resident pairs and the 2 moved ones are not included.

Table 5: Origin of own breeders (without faithful pairs)

	resident	moved	sum
♂	18	12	30
♀	7	12	19
sum	25	24	49

Before focussing on the moving distances of those moved or immigrated I will depict when the different categories were observed.

The portion of yearlings among the breeders oscillated between 0 and 33% (Figs. 19, 20). They appeared always in the years with increasing brood numbers but were scarce in years of stagnation. The influence of the preceding year (Fig. 21) seems to be small although the numbers might be correlated negatively. The figures 22 and 23 show further attempts to take this interpretation graphically. In

figure 23 the statement above on the appearance of yearling is evident.

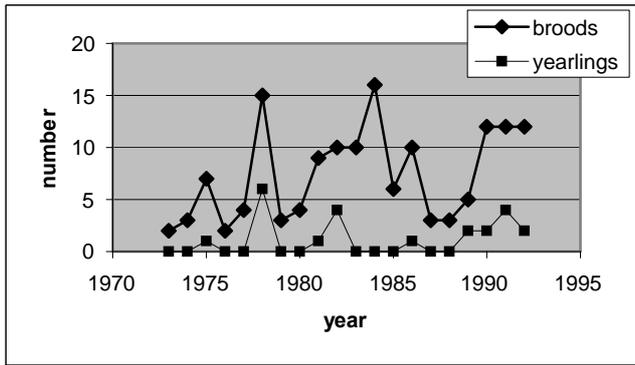


Fig. 19: The numbers of first broods and of yearlings per year

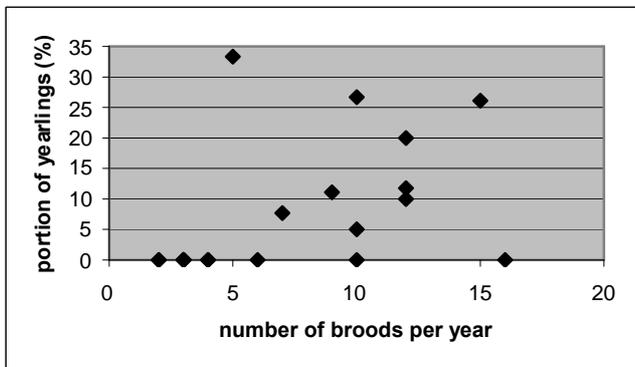


Fig. 20: Correlation between portion of yearlings and number of broods per year

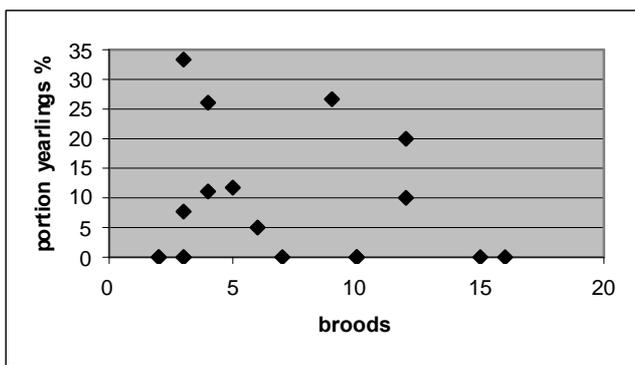


Fig. 21: Correlation between portion of yearlings (of exactly known age) in a year and number of broods in the preceding year

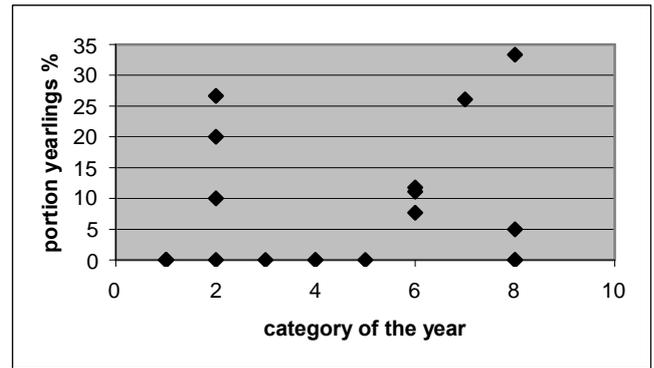


Fig. 22: Correlation between portion of yearlings and category of the year according to table 3

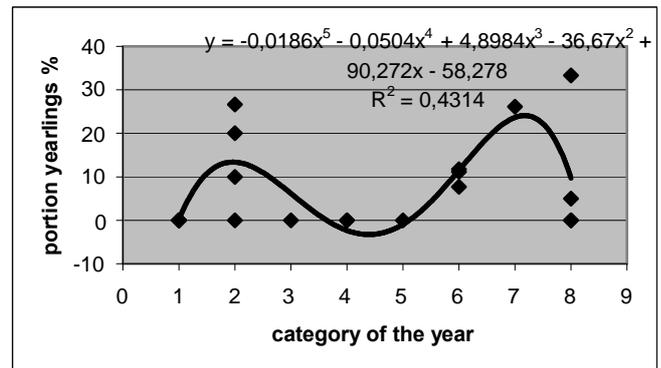


Fig. 23: Polynomial correlation between portion of yearlings and category of the year according to table 3

In the figures 24 and 25 giving the movements within the study area there is no tendency recognizable up to five broods, thereafter the portion of birds moved oscillates around 10%. This oscillation is strong at low brood numbers but weak at high numbers. Immigration from outside the study area was observed in most of the years (Figs. 26 and 27). The proportion scatters strongly around 40% at low brood numbers (up to 10) and ascends weakly to the higher brood numbers with then apparently less scattering. Looking at the resident breeders the impression is much similar but there is no ascending. The values scatter around ca. 27% (Figs. 28 and 29). According to the low numbers I did not discriminate between sexes.

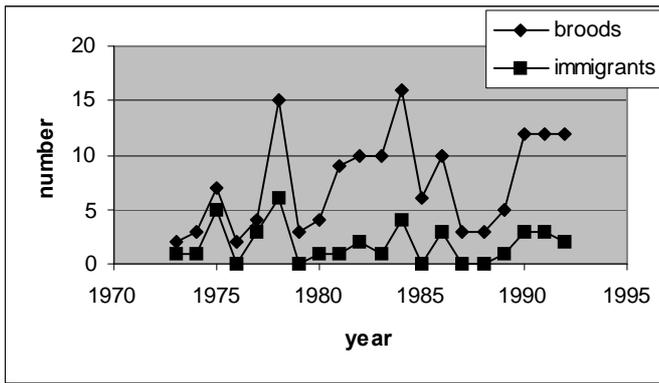


Fig. 24: Number of broods and number of breeders moved per year

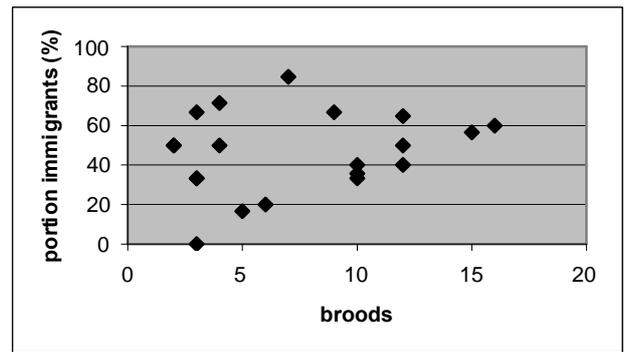


Fig. 27: Correlation between the number of broods of a year and the relative portion of immigrants of that year

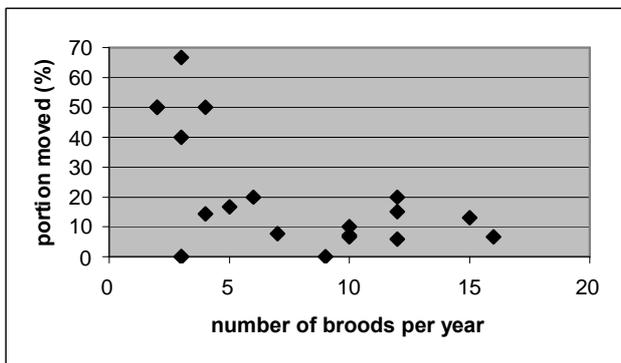


Fig. 25: Correlation between the number of (first) broods of a year and the relative portion of moved breeders of that year

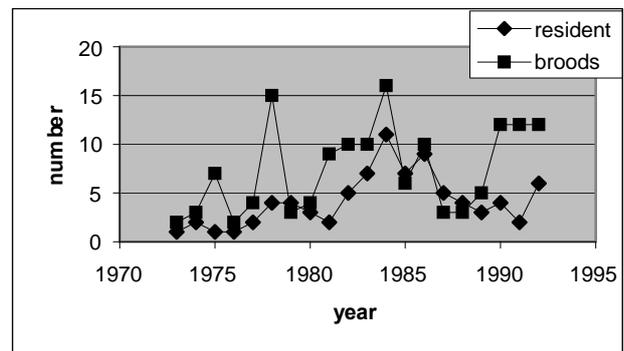


Fig. 28: Numbers of broods and resident breeders per year

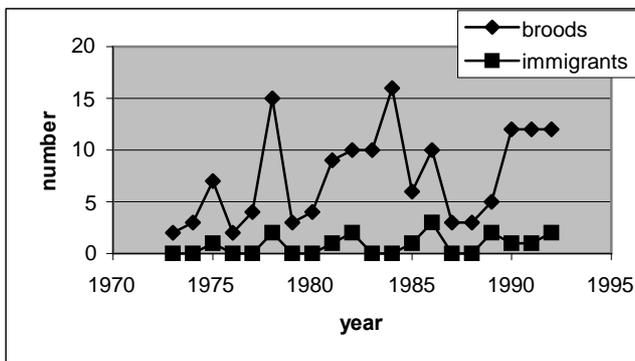


Fig. 26: Number of broods and immigrants per year

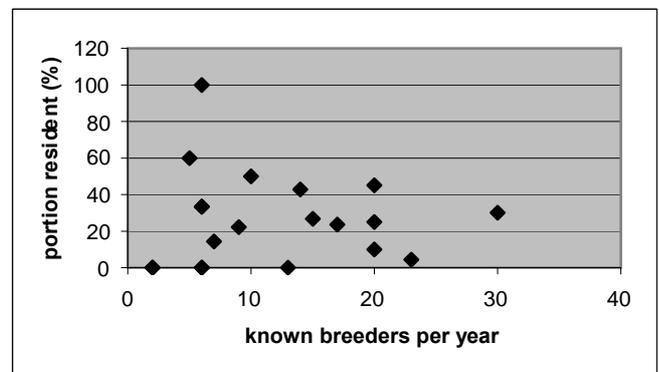


Fig. 29: Correlation between the number of broods of a year and the relative portion of resident breeders of that year

Both sexes used their chosen breeding sites for differing periods: the ♂ on average 1,5 years (SD 1,0, span 1-6) and the ♀ 1,3 years (SD 0,85, span 1-9).

We should still have a look at the distances travelled when moving or immigrating. (In the Figs. 30 to 32 the log values of the distances were chosen to avoid an unequal grouping and an over accentuation of the longer distances.) The yearlings (Fig. 30; N=21) showed a max at

about 1,7 corresponding to 56 km. For the adult breeders (without resident and moved pairs) both curves (Figs. 31, 32) – apart from the displaced maxima – are very similar. For the ♂ (N=11) the maximum is at about 0,6, meaning 4,0 km, in the ♀ (N=12) at about 0,8, meaning 6,2 km.

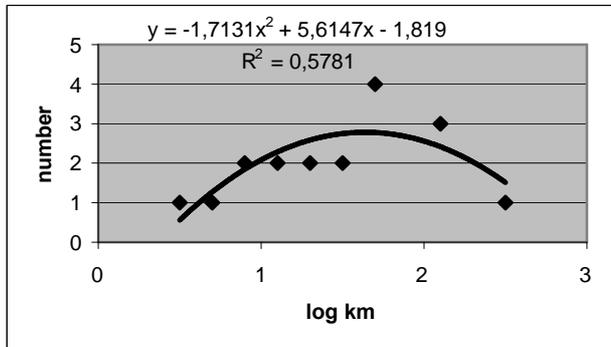


Fig. 30: Distance of origin of the breeding yearlings

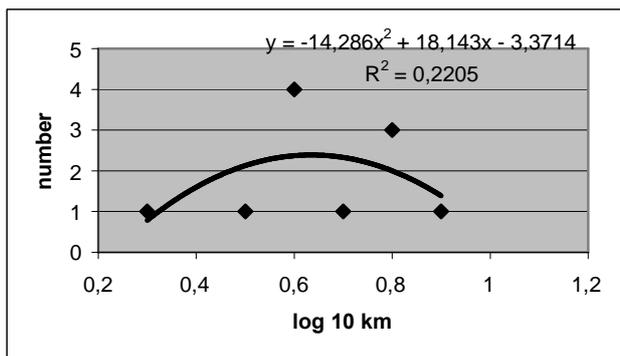


Fig. 31: Distance of origin of the known moved breeding ♂ (N=11)

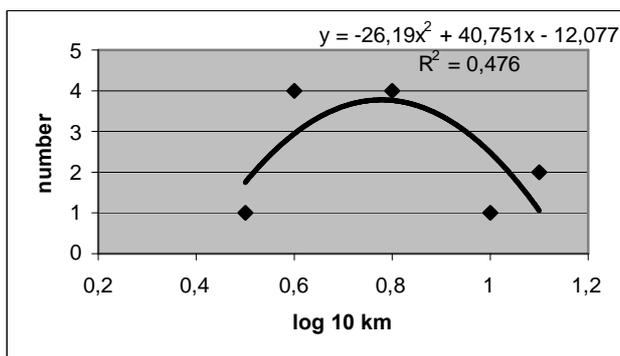


Fig. 32: Distance of origin of the known moved breeding ♀ (N=12)

3.4.2 Abode of the breeders

Ninety five (=58,6%), 41 ♂ (of 81;=50,6%) and 54 ♀ (of 80;=67,5%) of the altogether known breeders (162) of the years 1972 to 1988 (The last four years were omitted as those breeders

had a reduced chance of being recovered compared to the previous years.) were not recovered (here too second broods were omitted). The birds recovered had been resident (see table 6) or had moved within the study area. In the following the years 1989 – 1992 could be included as the interest was focussed on how the really recovered breeders had behaved.

Table 6: Whereabouts of the breeders of the years 1972 – 1991; “uncertain” means the mate was not controlled the year before or after the move; “loss” means loss of the mate.

	♂		♀		sum
	resident	moved	resident	moved	
total	42		31		73
uncertain	2	0	3	0	5
mate fidelity	13	2	13	2	30
mate loss	16	9	4	9	38
sum	31	11	20	11	73

In the row “mate fidelity” we find 15 pairs remaining together, two of them moved. Comparing only the numbers in the row “mate loss” of the total of 25 widowed or divorced ♂ 16 showed site fidelity, and only 4 of 13 in the ♀. So we may conclude that in the ♂ site fidelity is dominating. Though the part of birds which had moved was different in the sexes, table 6 allows to conclude also that loss of mate is the essential cause to abandon a breeding site.

We could guess that the decision to stay or to move was influenced by the success of the broods: Only two unsuccessful broods were found with known parents. In one of them none of the mates was controlled again the following years. The other one was a second brood. The ♂ of this pair was controlled no more, the ♀ was found as breeder for two more years. The data don't allow any conclusion.

Onto these birds which had been recovered as breeders the fate of 22 individuals is known. Six (3 ♂ and ♀ each) were found dead inside and 16 (7 ♂ and 9 ♀) outside the study area. On average the ♂ had moved 5,1 km (min 1,7, max 19 km), the ♀ 3,4 (min 1,7, max 7 km). In both sexes the sectors of the movements were W - ESE and only once NW.

3.4.3 Pairs

Breeding barn owls practise a very strict sharing of parental duties. Therefore the success of the broods never is depending on only one bird but always on a pair. So the pairs were studied as unities. From the total of 152 broods both mates were known in 111.

3.4.3.1 Properties of pairs

Seventeen of the 19 pairs which were controlled in the study area for two consecutive years held their breeding site, two moved. So we can be certain that pairs which breed together for a second time stay at their old breeding site if possible. There is no information about the eventual causes for the movements of the two pairs which had moved.

3.4.3.2 Mate fidelity

After BLACK (1996:14) the case that both members of a pair again are registered the following year is called one pair year. Following this definition 22 pair years were registered (data from the surroundings of the study are included). In this number included is only one case of divorce (this after a successful brood with 4 fledglings against 4,67 ones in the remaining three broods of that year). With the reservation that there were one or more divorces which had not been detected for one mate had moved outside the study area these numbers hardly allow any doubt on the principle of life long partnership. This interpretation also is underlined by the movement of two pairs.

In 96 broods both mates were known and the broods were estimated being first broods for both mates. In these broods 54 ♂ and 69 ♀ were engaged. All years together the ♂ had 36x1, 13x2, 3x3, 1x4, and 1x6, on average 1,5 mates. Vice versa the ♀ had 60x1, 7x2, 1x3, and 1x4, on average 1,17 mates.

For second broods and bigyny see 3.5.1..

3.4.3.3 New pairings after loss of mate

As naturally there are always more younger unmarried or widowed owls, middle old or old birds of both sexes mostly find apparently younger mates when remarrying (Tab. 7). Accordingly the mates of yearlings on average are older than these themselves, even though five times yearlings bred with yearlings.

Table 7: Mean values of the age of former and new mates of the breeders

	yearlings		middle old			old		
	N	partner	N	partner old	partner new	N	Partner old	partner new
♂	13	1,48	28	2,61	1,93	9	5,70	2,33
♀	8	1,42	16	2,55	1,98	7	5,31	2,43

It seemed possible that mates would not find totally by chance but that for unknown reasons the owls would look for mates of same or perhaps similar age. So we studied the age composition of newly formed pairs (age groups see 3.4). Basing on the 82 newly formed pairs, both mates of which were known by age, age combination by chance would lead to the following numbers (Table 8):

Table 8: Portions (%) of age groups in newly formed pairs as expected when combined by chance

	yearlings ♀	middle old ♀	old ♀	sum
yearlings ♂	44,04	7,69	5,59	57,32
middle old ♂	24,36	4,25	3,09	31,71
old ♂	8,43	1,47	1,07	10,98
				100,00

Table 9: Actual portions (%) of age groups of newly formed pairs in the population

	yearlings ♀	middle old ♀	old ♀	sum
yearlings ♂	46,34	6,10	4,88	57,32
middle old ♂	23,17	6,10	2,44	31,71
old ♂	7,32	1,22	2,44	10,98
				100,00

The comparison between tables 8 and 9 clearly demonstrates that there must be an age biased selection for mates: All three combinations of similarly aged mates (screened areas) in reality are more frequent than in combination by chance. Consequently all other numbers are smaller in reality.

It was examined whether the birds used the loss of a mate (regardless by which reason) to find a better one. The life production of fledglings of the lost partners was compared to that of the new ones. (The numbers of table 10 slightly differ from those in table 6 as not for all individuals sufficiently data on their mates were available.) It becomes visible that after the loss of mate (though the values scattered obviously) ♂ as well as ♀ succeeded in finding a better mate, the ♂ more by staying, the ♀ by moving.

Table 10: Averaged difference in mate quality (life production fledglings) between new and former mate after loss of mate and finding a new one, separated for resident and moved breeders (see text)

	♂		♀	
	number	gain	number	gain
stayed	15	2,93	3	0
moved	11	1,09	8	4,00
sum	26	2,15	11	3,00

3.5 Breeding success / Quality

3.5.1 Quality of breeding sites

It seemed interesting whether the different success values of the broods are in any connection to the preference of the breeding sites established above. The total number of broods at the actual agglomerations were taken as measure. The average egg numbers (Fig. 33) and the average numbers of fledglings per village (Fig. 34) seem to diminish with the preference of the latter. Figure 35 doesn't give any support for a density dependence of the egg numbers. The same matches for the numbers of hatchlings and fledglings (no Figs.).

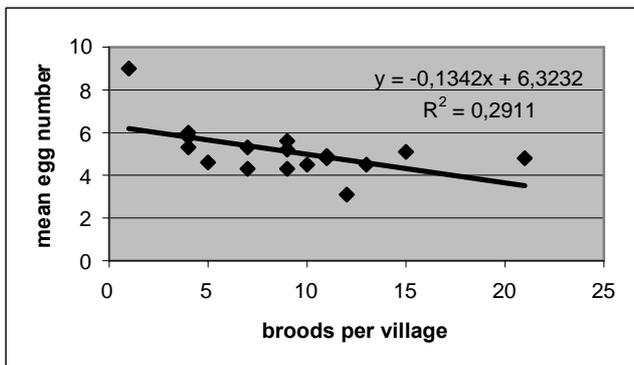


Figure 33: Egg numbers depending on the number of broods per village

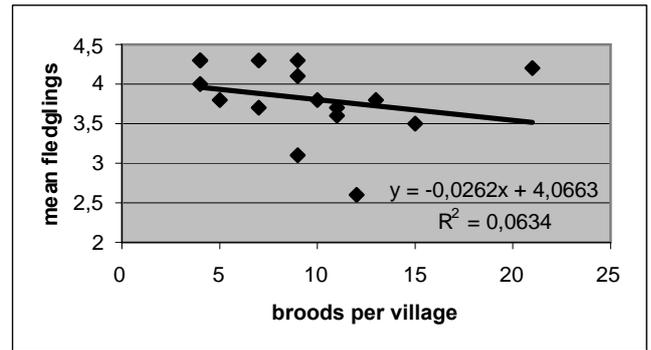


Figure 34: Number of fledglings depending on the number of broods per village

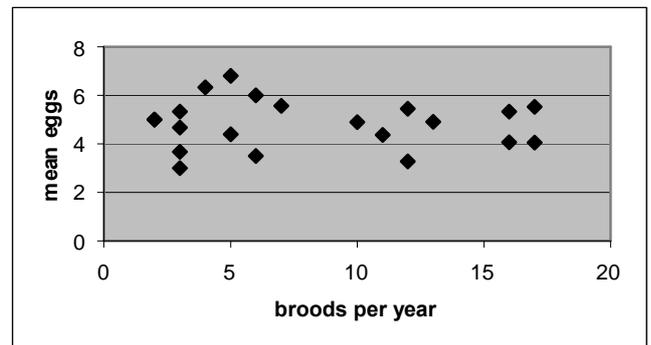


Figure 35: Egg numbers in relation to the number of broods of the year as a measure of the breeding population density

3.5.2 Quality of breeders

Living creatures generally are of differing quality. Certainly it is of great importance for individuals willing to reproduce to find a mate of the highest possible quality. Out of the measurable characters being at the disposition of a human observer for this purpose the breeding success (measured as life productivity) and the mean number of fledglings per brood were taken.

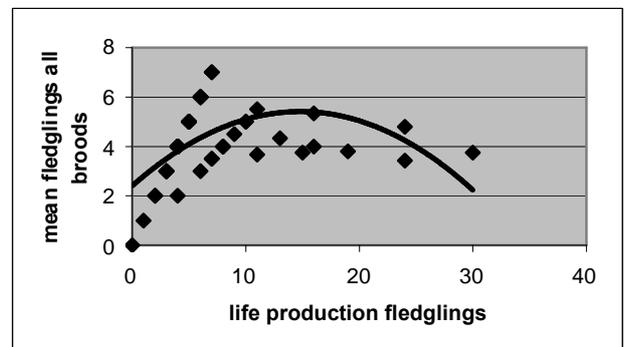


Figure 36: Correlation between life production and mean numbers of fledglings of their broods in 116 ♂



Figure 37: Correlation between life production and mean numbers of fledglings of their broods in 126 ♀

At first we see in the figures 36 and 37 that life production of the ♀ is less than that of the ♂, a consequence of the higher longevity of the ♂. The obvious arrangement of the values in rows has a simple explanation: The first row at left is the quantity of all those which breed only once, in which life production is identical with the mean per brood, and of those which were totally unsuccessful (in the origin), regardless of how many breeding attempts they had. Then we see the row of those having made two broods. And this arrangement should be continued if there were enough values. The binomial regression curve could make guess that the mean values of fledglings increase up to a life production of about 14 – 15 fledglings and decrease thereafter. Some birds reach that value in one season (with first and second broods), some need several years.

3.5.2.1 Breeding success and age

For many bird species it has been established (Curio 1983) and it is imaginable for barn owls too that breeding success is dependant on age (and/or breeding experience). A first comparison between yearlings and older birds of both sexes is shown in table 11.

Table 11: Comparison of the breeding success between yearlings of known age and certainly older birds (successful broods only)

breeding success (fledglings)					
		♂		♀	
	N	mean	N	mean	
yearlings	11	4,64	10	4,4	
older	52	3,92	39	3,85	

The numbers seem to prove that the yearlings of either sex breed more successfully than older birds. But as demonstrated in chapter 3.4.1,

yearlings do not breed all years. So it is necessary to compare the breeding success of yearlings with that of older birds only in the years with breeding yearlings. If we take only these years the yearlings remain more successful, but the difference is less (Tab. 12).

Table 12: Comparison of the breeding success (fledglings) of yearlings of known age with certainly older birds in years with breeding yearlings

breeding success (fledglings)					
		♂		♀	
	N	mean	N	mean	
yearlings	11	4,64	10	4,4	
older	30	4,17	28	4,18	

The breeding success of all older birds seems to decrease continuously (linear regression: Fig. 38). If a polynomic regression is used instead a general pattern results independently of the sex and thereof whether the age of the birds studied is known exactly or only approximately (see chap. 3.4). The breeding success declines for two to four years, then inclines and again declines. In the ♀ the amplitude is greater than in the ♂. The yearlings exactly fit that image. If we look only at the birds of exactly known age merely the positions of the minimum and the maximum slightly shift. Astonishing enough the amplitude of the owls with exactly known age is less than that of the birds with only approximately known age.

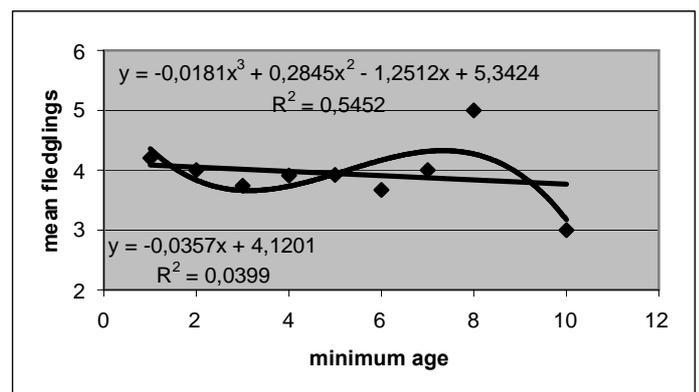


Fig. 38: Dependence of breeding success (fledglings) on age (all owls known by exact or approximate age, N=238)

The higher breeding success of the yearlings being clearly visible could depend on the existence of two different life strategies: (1) to concentrate on the success of this first and

perhaps single breeding attempt or (2) not to spend all just in this first year but to count on more years as breeder. In fact in table 13 we see a difference in the success numbers of these two hypothesized strategy variants in the first year.

Table 13: Comparison between the breeding success of yearlings breeding only once with that of the first year of multiple breeders

		N	eggs	hatchlings	fledglings
single breeders	yearlings	9	5,78	5,22	4,44
	ca. 1 year old	23	5,35	5,04	4,26
	sum	32			
	mean		5,47	5,09	4,31
first year multiple breeders	yearlings	3	3,67	3,67	3,67
	ca. 1 year old	40	5,20	4,65	4,10
	sum	43			
	mean		5,09	4,58	4,07

The comparison of the yearlings with the two other age groups (Fig. 39) confirms the image of table 11. The decline in the egg production from the yearlings to the middle aged breeders already had been visible in the trinomic regression line in figure 38 as well as the new incline towards higher age. This new incline is clearly visible in the ♀ but lacking in the ♂.

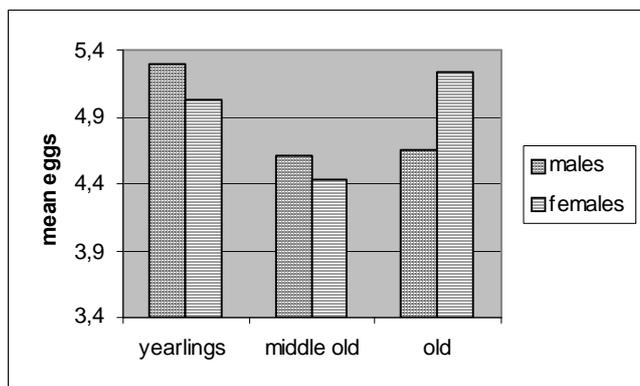


Figure 39: Influence of the age groups on egg production

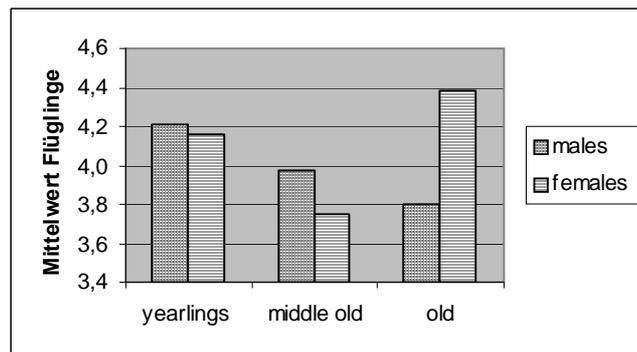


Figure 40: Influence of age groups on fledgling numbers

The initial supposition these differences also should appear in the fledgling numbers seemed to be confirmed (Fig. 40). Here the efficiency decline with inclining age is very prominent in the ♂. It seemed interesting to know whether the differences in productivity between the sexes and the age groups were different in the stages of the breeding process.

The difference between the age groups persists regarding hatching success (Fig. 41).

Nevertheless the influence of the age groups during incubation is fairly different (Fig. 42). No doubt, the middle old breeders are the most successful ones. During this stage the yearlings are clearly worse than the other groups. The contribution to the success in this stage of breeding obviously increases in both sexes with age and then again decreases.

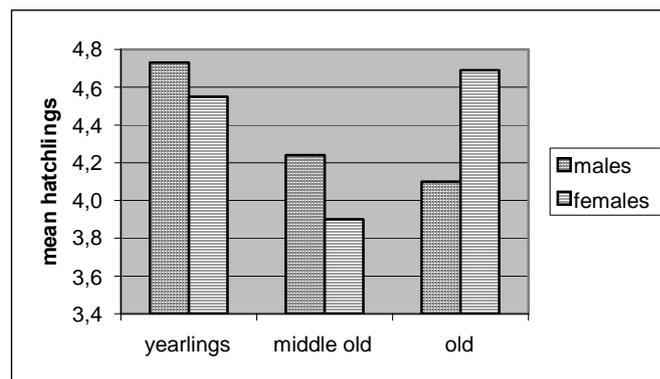


Figure 41: Hatchlings of age groups

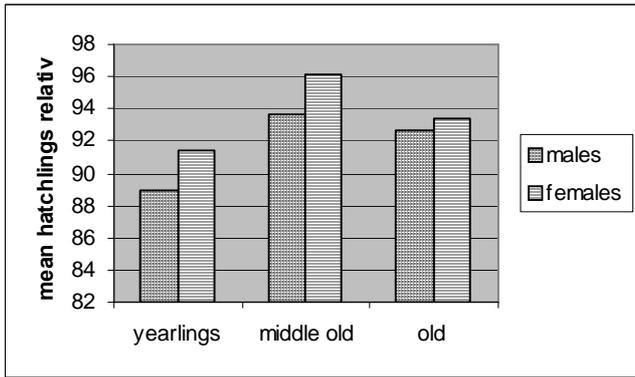


Figure 42: Hatching success of age groups in relation to egg number

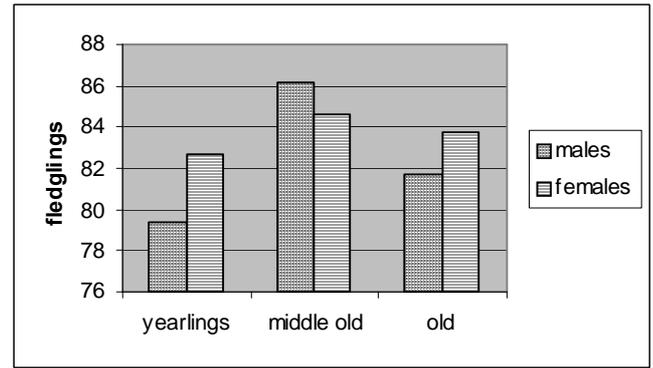


Figure 44: Number of fledglings per 100 eggs by age groups

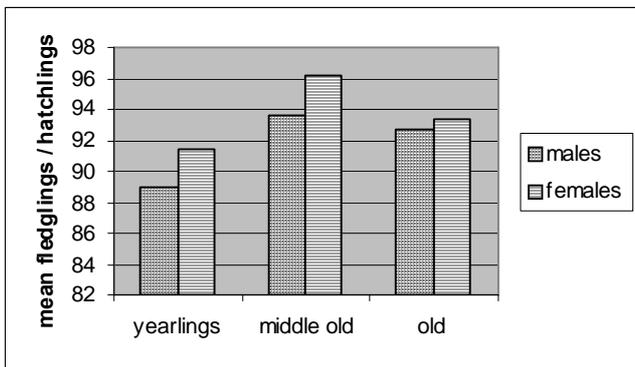


Figure 43: Fledging success of the age groups in relation to the number of hatchlings

Incubation of the eggs is followed by brooding. During this period again the middle old breeders are the better ones and the yearlings the worse ones (Fig. 43). Compared to the incubation period the image of the relations has not altered. The performance balance of the sexes and the age groups is most clearly visible in figure 44, showing how many fledglings are produced on the basis of 100 eggs. Without any doubt the middle old breeders are the most effective and the yearlings the most ineffective ones. But indeed the prominence of the yearlings basing on their egg numbers (see tables 10-12 and Fig. 39) is great enough to predominate in the mere success balance. Die differences in efficiency are greater in the ♂ than in the ♀.

These differences in performance will be further studied in chapter 3.5.3 under the aspect of partner combination.

3.5.2.2 Breeding success and mate fidelity

The breeding success (fledglings) of 17 faithful pairs was on average 4,06 (all pairs were successful) in their respective second year of the pair bond, that one of 80 new successful pairs 4,18; if we here add the four not successful pairs this value is 3,99. These 17 faithful pairs had a success of 4,24 the respective preceding year (There too all were successful).

3.5.2.3 Breeding success and laying date

For 93 broods of the first half of the year the laying date was known or could be deduced from the age of hatchlings. There we used a constant laying distance of two days and an incubation period of 30 days. 87 of these broods were successful. As shown in figure 45 the laying date could delay with an increase in the quality of the year.

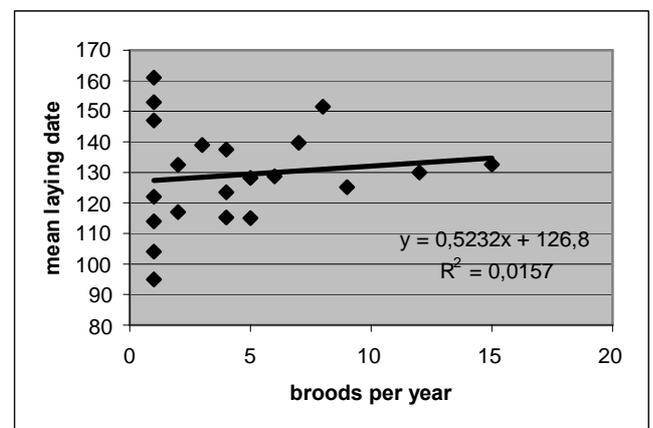


Figure 45: Correlation between number of broods of a year and the mean laying date

The mean clutch size in dependence of the mean laying date of a given year is shown in figure 46: In years with later laying dates the numbers of eggs in first broods are greater.

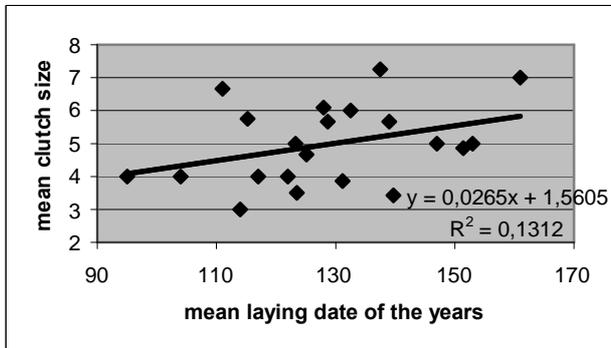


Figure 46: Mean clutch size depending on mean laying date of every single year

But if we look at clutch size in its dependence from the laying date irrespective of the year a different aspect becomes visible (Fig. 47). With the ongoing of the year the mean clutch size diminishes. But as the binomic trend line shows, this tendency does not seem to be linear.

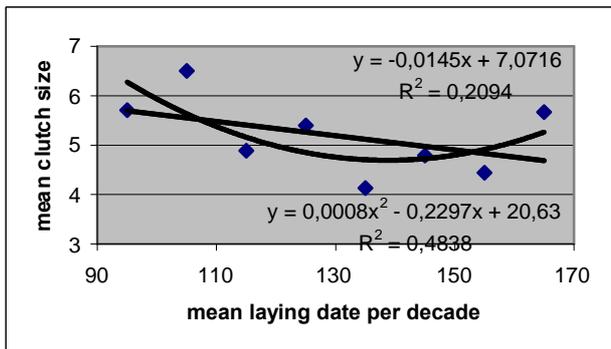


Figure 47: Decline of clutch size in the first half of the year depending on the laying date (days after New Year; decades) (all years together)

The mean number of fledglings too diminishes with the date of egg laying and later increases again (Fig. 48). But here the non linearity is still more prominent.

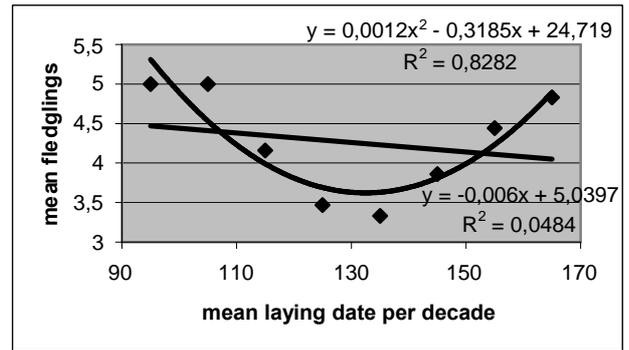


Figure 48: The alterations of breeding success in the first half of the year depending on laying date (all years together)

The interrelation between the age of the ♂ breeders and the laying date is shown in figure 49. The older ♂ are beginning first with breeding and therefore are responsible for the higher values. This holds also true for the ♀ (no Fig.).

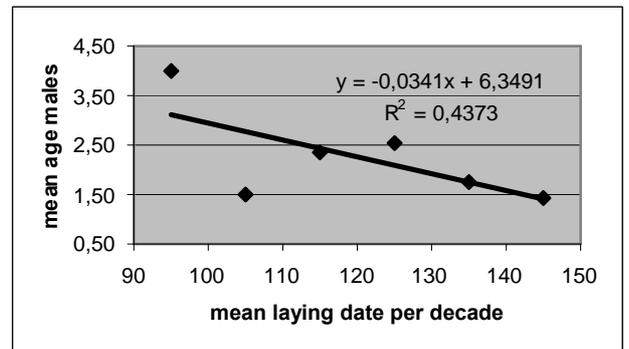


Figure 49: Laying date depending on the age of the ♂. The single points represent means of at least 20 ♂, point 2 indeed of only 3.

3.5.3 Quality of pairs

Above I demonstrated (chap. 3.5.2.1) that breeding success is depending on the age of the individuals inclined. Though apart from the yearlings mating by age does not seem to be usual we studied whether there are favourable or unfavourable partner combination by age. So the breeding success of all nine possible combinations were examined.

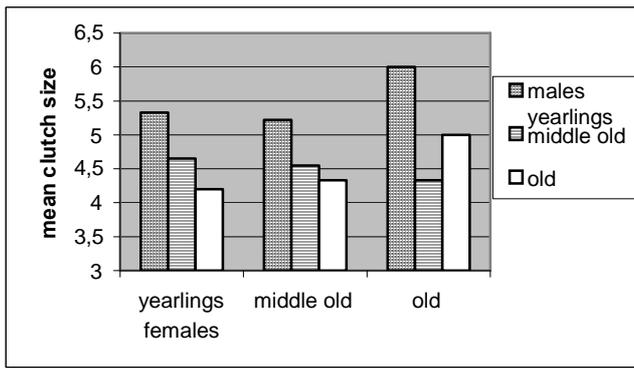


Figure 50: Egg production of pairs by age combinations; N=110

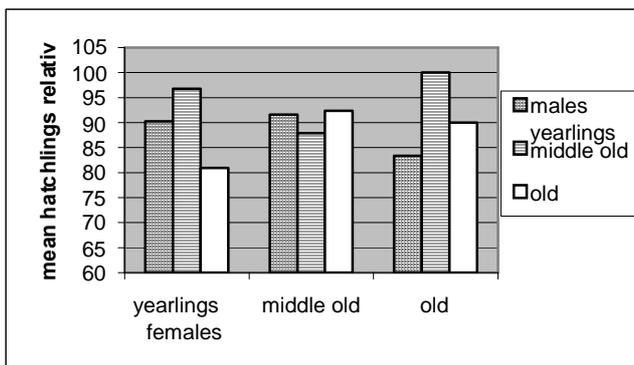


Figure 51: Hatching success of the age combinations in relation to clutch size

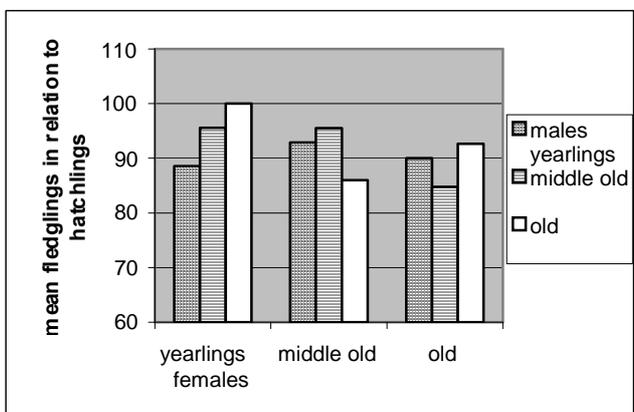


Figure 52: Fledging success of the age combinations in relation to number of hatchlings

Young ♂ have the greatest influence on clutch size, especially mated to an old ♀ (Fig. 50). The influence of the middle old ♂ decreases with increasing age of the ♀. Quite different regarding the old ♂: Their influence increases with increasing age of the ♀. Seen from the ♀ side: Young ♀ (yearlings) produce most eggs mated to a young ♂, meaning to a ♂ of equal age. Egg production decreases with increasing age of the ♂. The latter fits for the middle old ♀ as well. But here the advantage of similar age is

missing. Old ♀ reach their best egg laying capacity mated to a yearling. Mated to a middle old ♂ they are much less productive but the value again increases remarkably when mated to an older ♂.

As we did regarding the capacities of the age groups of both sexes (s. chap. 3.5.2.1) so we should here study where in the other phases of the breeding event which age combination has special advantages or disadvantages. Yearling ♂ (Fig. 51) at least mated to a yearling or middle aged ♀ do have a clear influence on the hatching rate, but less mated to an old ♀. The best results we see in the middle aged ♂ mated to yearling or old ♀ but not to similar aged ones (as seen in the egg production). Old ♂ are worse mated to a yearling, best mated to a middle old and slightly less good with a ♀ of same age.

The description of the sex role in the incubation phase shall be described seen from the ♀ perspective (fig. 52): Yearling ♀ manage this task best mated to an old, worse mated to an similar aged ♂. Old ♀ cooperate best with ♂ of similar age, worse with middle aged ones.



Figure 53: Fledgling production of the age combinations

Looking at the breeding success altogether (fig. 53) we may state that there are life age combinations whose success (fitness) clearly stands up against the remaining ones: yearling ♀ with yearling or middle old ♂, middle old ♀ with yearling ♂, old ♀ with yearling or similarly old ♂.

As the production of eggs without doubt is costly we may also ask: Who produces his fledglings with a minimum of eggs? Figure 54 shows the clear winner. Yearling ♀ mated to middle old ♂. Then follow, but already with distance, narrow

together the yearling ♀ with yearling or same age ♂ and the old ♀ with middle old or same age ♂. All other combinations need distinctly more eggs.

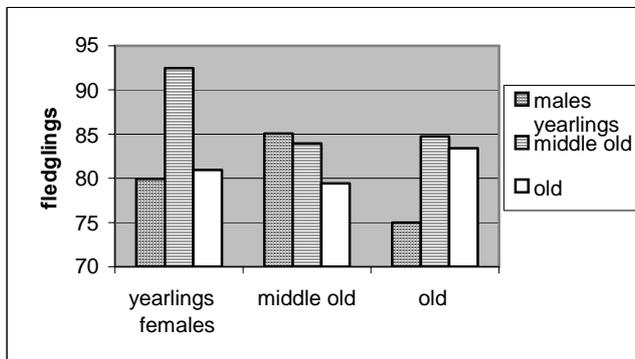


Figure 54: The success of the age combinations during incubating of 100 eggs and rearing the resp. hatchlings

3.5.4 Success of second broods

The success of the five second broods (s. 3.4.1.) with a mean of 2,33 fledglings was clearly beyond the means of these years (s. tab. 7).

3.6 Alterations in the population

The totality of the population indeed mostly consists of the breeders but is not identical with these. There is still existing the difficultly identifiable group of non breeders (brood reserve: KAUS 1977). Here we only adjoin those individuals to this group which have been controlled unless we could record the participation at a brood.

3.6.1 Dynamics

Figure 55 shows the attempt to summarize the movements within the study area, those from the inside towards the not controlled surroundings, those from the outside into, and the increase by births in the shape of a schematic life table (BEGON et al. 1996). At virtual time 1 there do exist the two compartments (subpopulations) "breeders" and "non breeders". The numbers shown (222 and 2 resp.) mean the sums of the basic years 1 (1972) to n-1 (1991). The real content is the numbers of individuals ringed and controlled. The numbers in the arrows mean the movements from one compartment to the other from the basic years to the end years. The latter ones are the years 2 (1973) to n (1992). To facilitate comparison to similar studies in the following also probability values are given.

Breeders and non breeders together build the virtual population size 224 (or as basic probability: 1). Seventy two of the 222 breeders survived to the following year. That means a probability of 0,32 (based on N=224) or expressed differently: On average in the n study years 32% of the breeders of a year survived to the next one and breed again. One during these n years (0,004) survived as well but did not breed the following year. Three died within the study area (0,013). A greater number (16; 0,07) was not controlled in the study area during the following year but later was found outside: They had emigrated (details see chap. 3.4.2). Further 26 (0,12) were controlled as breeders in the study area in later years. Here they are classified as temporarily absent. Probably some of them were non breeders, hence present. Of course they are again included in the number of immigrants (142; 0,53: based on the basic population of 224). So we had 116 real immigrants (0,52). In the number of immigrants included are four recruits who did not breed as yearlings but later. Some of these too could have been present as not recognized non breeders. Not shown is the loss of 132 breeders which had emigrated or died inside the study area without record.

To summarize, the breeding population had the following composition:

- 30% resident
- 11% again present after temporary absence or presence unrecorded
- < 1% recorded as non breeders the preceding year
- 10% own recruits
- 49% real immigrants

The left side of figure 55 shows the increase of the population by births. The 222 known and 14 unknown breeders (of atotal of 118 broods) altogether produced 582 eggs. That means an average clutch size of the single bird of 4,93. Then there are depicted the real numbers of hatchlings and fledglings and in the arrows the probabilities to reach the next stage. Eighty one of the 469 fledglings (0,16 based on the total number of fledglings) emigrated. They later were recorded outside the study area. Further 23 (0,04 again based on the total number of fledglings; based on the basic population: 0,1) appeared in the following years as breeders ("recruits") in the study population.

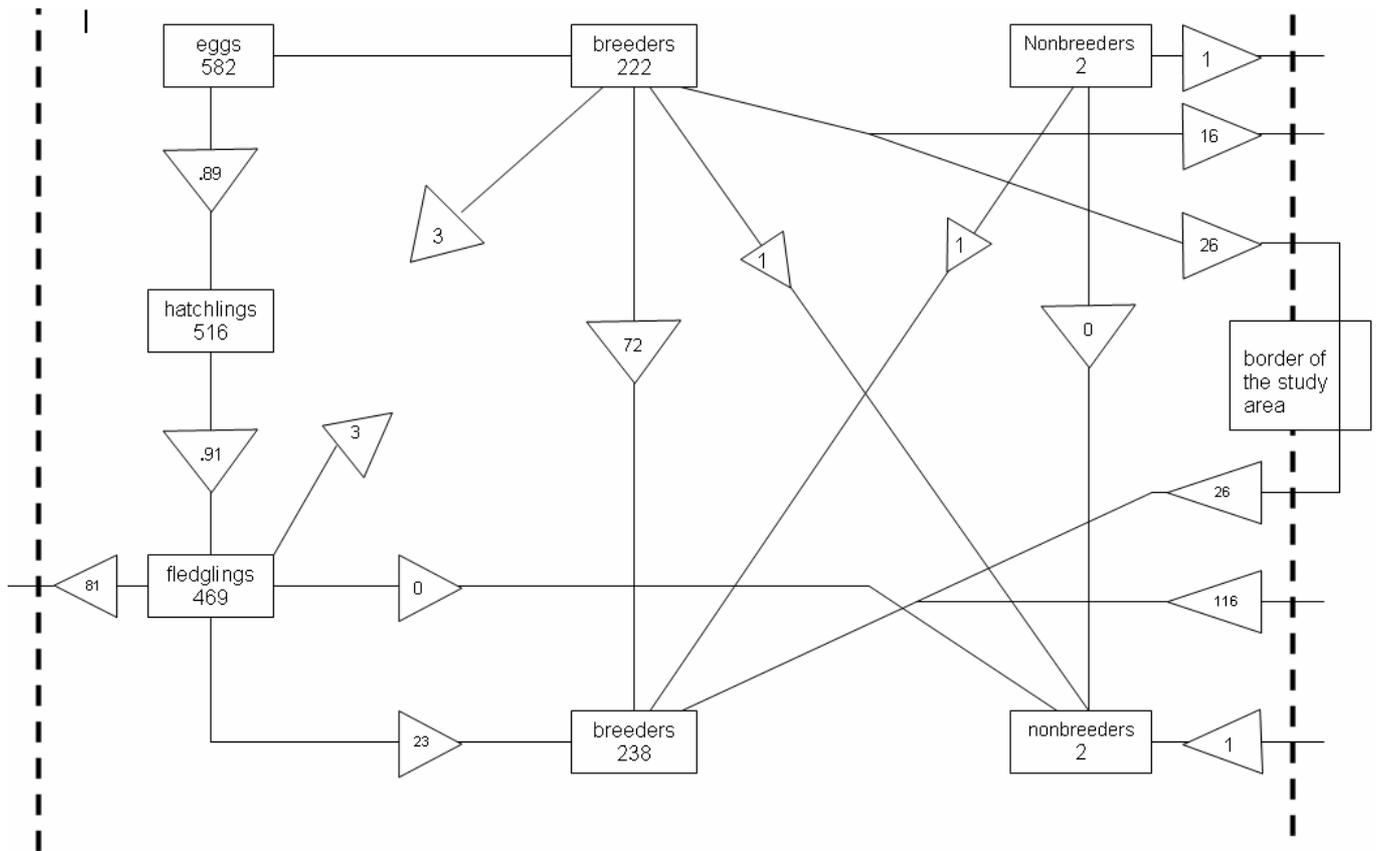


Figure 55: Schematic life table of the barn owl population of the study area: all 21 years summarized. For further explanation see text.

From the alteration numbers in figure 55 a population of 240 (1,06) individuals for the end year results. That means translated: On average the population increased for about 6%. This number well agrees with the increase of broods in figure 15 (s. chap. 3.3).

3.6.2 Mortality

The reduction of the population by mortality is a substantial factor in understanding population dynamics. In the following the time from hatching (birth) to the end of march of the following year is counted as first year of life. All further life years count from April to march. Mortality rates of the complex process "birth" already are found in figure 55. From egg stage to hatching mortality is 0,11 (1 – 0,89), until fledging again 0,08. After this stage we have to find a new basis for all calculations as the fate of about 80% of the fledglings is unknown: One hundred and three of the really known 107 individuals (81 emigrants + 23 recruits + 3 found dead in the study area) could be used and taken as new basic entity. The mortality of these has

been studied by a conventional life table (BEGON et al. 1996). There the study by years (or cohorts) was not possible due to the small numbers. All years were summarized (Tab. 14). One bird which reached 14 years is not considered. Besides an increased mortality during the first year the graphical representation of age and k-value (Fig. 56) hardly represents any dependence on age only the numbers beginning with year two are taken, an obvious increase of mortality with age is resulting (Fig. 57).

Table 14: Conventional life table of all birds in the study area known by age (a_x number of individuals living at time x ; l_x values related to 1000; d_x decrease of living individuals from x_n to x_{n+1} ; q_x mortality d_x/l_x ; $k_x = \log_{ax} - \log_{ax+1}$)

age	living				
x	a _x	l _x	d _x	q _x	k _x
1	103	1000,00	592,23	0,59	0,39
2	42	407,77	174,76	0,43	0,24
3	24	233,01	77,67	0,33	0,18
4	16	155,34	77,67	0,50	0,30
5	8	77,67	9,71	0,13	0,06
6	7	67,96	29,13	0,43	0,24
7	4	38,83	19,42	0,50	0,30
8	2	19,42	9,71	0,50	0,30
9	1	9,71	0,00	0,00	
10	1	9,71			

could not be prolonged to April as there were no values.

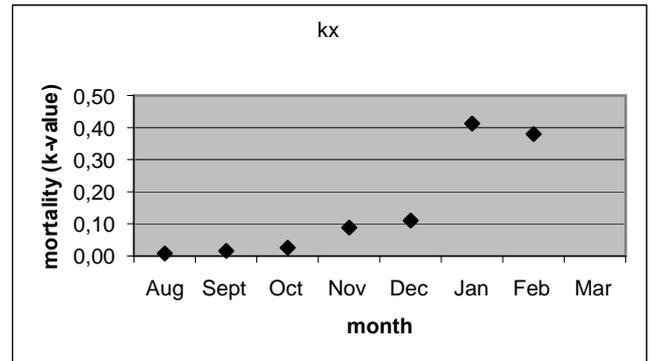


Figure 58: Mortality of young barn owls during their first year of life

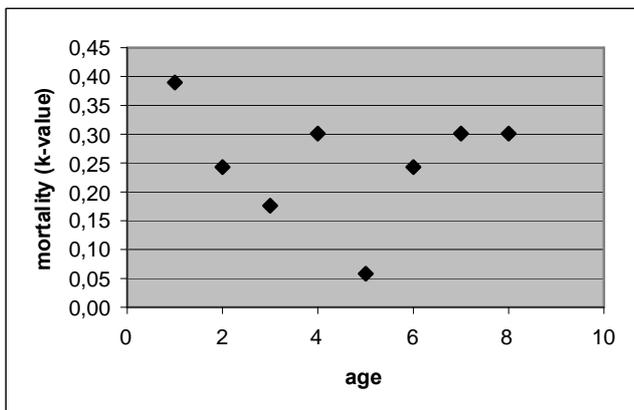


Figure 56: Mortality depending on age; values from tab. 14

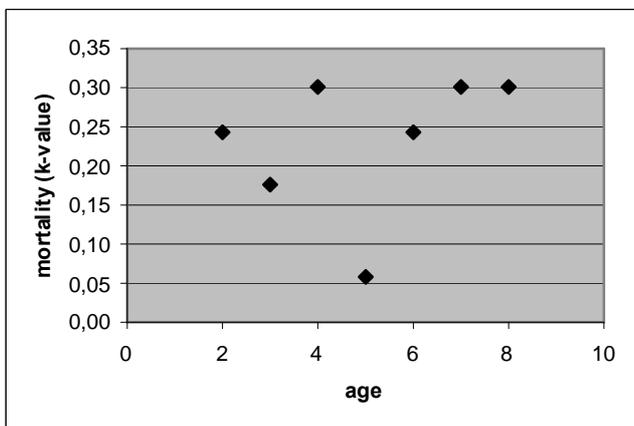


Figure 57: Mortality depending on age; birds older than 1 year; values from tab. 14

Looking at details of mortality during the first year of life we see: In August (again all years summarized) 55 of all individuals which had died during their first year were living. This number is the basis for a new life table. So it can be demonstrated (Fig. 58) that mortality slightly increases up to December, then steeply up to January, and then decreases again. The curve

3.6.3 Dispersion

Juvenile dispersion will be studied later, for that of the adults see chapter 3.4.2.

3.6.4 Productivity

Different from the chapter “breeding success” here will be communicated in which extent the local breeding population of a year had contributed to that of the following year, at least as far as is recorded. For this purpose three values were added: the really recorded recruits in the population studied and the breeders recorded or guessed inside the study area. Like in the chapter “mortality” here it is assumed for the latter ones that individuals found later than March 31st do belong to the breeding population. Thus we have to add one young bird found dead in the study area after this time limit to the 23 recruits. The resulting 24 individuals are the contribution of the breeding population to the next one or a factor 0,1. Expressed otherwise: Ten percent of the breeders were descendants of the local population.

3.6.5 Balance

The summarizing presentation in figure 55 possibly can narrow to reality. It only represents the whereabouts of 41% of the (virtual) basis population and the origin of the resulting one. It seems impossible to present a real balance as the reliability of the different values is extremely different. Basing on the intensive controls the identity of the breeders of the different years is known to a mean of 79,8%. All depending values thus are fairly certain.

4. Discussion

The results presented here mostly are based on relatively small samples and thus they burdened with more or less great uncertainties. By the same reason statistical treatment often seemed not useful. So we mostly dispensed with. Thus the results often merely are trend statements and cautious interpretations. But as the studies spanned over a relatively long period with a constant method and especially because the portion of adult birds controlled hitherto has not been reached in central Europe, the results are estimated being worth communication.

4.1 Breeding sites

The rank of the single breeding site which had been deduced from the numbers of broods being performed there could contain a fairly great hazard factor because a greater number of the breeders had no real choice: (1) as a consequence of the small number of boxes and (2) because they eventually arrived late in the study area and then found most of the boxes already occupied. So they had to take the first box they found being free. But when breeding there they had a lot of time to compare the quality of their boxes to that of neighbouring ones. The result of this comparison only could become valid when - before the following brood - they had to decide: stay or move. We found a rank order of the boxes very similar to that we derived from the total number of broods there when we took the time the individuals used a single box and also when using the popularity of a box as moving destiny.

The preference on moving became visible although the preferred boxes in part were certainly not at disposal for these were also those with the longest occupation time. So the number of broods at a site is a good measure for the quality of that site. Of course it remains open wherein the latter really consists.

The longer staying time at a site of higher rank is one of the basis' of this rank. Seen from the level of the breeders we might guess that they here live longer and consequently do breed here more often. But the opposite is possible as well: The more vital owls which more often succeed in occupying the better breeding sites, have a greater longevity. So they breed more often.

4.1.1 Choosing a breeding site

It is obvious that surviving breeding pairs nearly always stayed at the site of the preceding year. Nevertheless the loss of the mate causes 47,4% of the breeders to desert the former breeding

site. Indeed 64% of the ♂ do stay even after the loss of the mate, but only 30,8% of the ♀. That means for those who stayed that they voted for the old site and against the search for a new one.

All who left their old breeding site, and the newcomers as well have to look for a (new) breeding site. Certainly they do not – except the own recruits – take the next best one: Movers inside the study area – two pairs included – as well as immigrants show a preference for the better sites. That indeed means that they must well look around before their decision. Otherwise there could be no selection. As communicated by SCHNEIDER & ECK (1977) and EPPLE (1985), the males are the sex to arrive first at the breeding site. (Here indeed free breeding sites in church towers were studied.) Accordingly it should be them to have the first choice.

Somehow contradicting are the findings of TAYLOR (1994) and ROULIN (1998) who during winter (ROULIN: mostly during February) found birds of ether sex, more often indeed ♀ and not to rarely several birds at a time in the boxes. SHAWYER (1998) too found pairs roosting together over winter in the boxes. He expressively writes: “Young female birds seem to arrive at their future breeding places first” (1998: 94). But “For single birds whose mates have not survived the winter and at newly provided sites such as nestboxes, it is sometimes the male bird which arrives first” (SHAWYER 1998: 107).

These contradictions could be interpreted as follows: Most free breeding sites are almost unsuitable as winter roosts for they have only a weak sight protection. Probably they are visited occasionally but that remains undetected. Totally different the boxes: Certainly they are best wind protected roosting sites. But in springtime they loose this function. Then the interpretation by the owls changes: Now the function as breeding sites comes to the foreground. And then they are already known to a larger number of owls. Now the ♂ well visibly and audibly announce their claim, even if they were not the first ones at that breeding site (so likewise EPPLE 1976 for his captive birds). For ROULIN (1998) these winter roosts in the boxes only do serve to maintain the claim for the breeding site.

4.2 Quality of years

It is especially interesting that despite all oscillations from year to year during the time of the study an advance of the laying date becomes visible. This phenomenon already has been stated by other authors for very different bird species: KANIA (1994) for Great and Blue Tits in Poland, WINKEL & HUDDE (1997) and WINKEL (2002) for Great and Blue Tits, Nuthatch, and Spotted Flycatcher, LUDWICHOWSKY (1997) for the Goldeneye, and MCCLEERY & PERRINS for 64 of 65 bird species in Britain. This indeed could depend on the climatic changes. In the barn owl this advance also was detected in other breeding areas in Germany (KNIPRATH et al.; 2007).

In worse years the age of the birds on average is higher than in better ones. Simultaneously in the latter ones the laying date is later. This can be explained by the fact that the older birds begin laying earlier. Of course this does not mean that the older birds begin their broods earlier in worse years. They always do so. But in worse years this fact is more obvious because then there are relatively more older breeders. The Question why the birds are older in worse years will be discussed later.

4.3 The breeders

The portion of 10% recruits in our breeding population calculated here is far beyond the 37,5% (for Liemers) and the 50% (for Achterhoek) that were found by DE BRUIN (1994) for these two populations in the Netherlands. Of course DE BRUIN gives a portion of immigrants of <10%. In the population studied here this portion on average was 49% (s. figs. 27 and 55).

In figure 30 the mean distance of origin of the recruits (own and immigrated ones) is near 52,5 km. These values indeed must be explained. Nine of these birds originate from distances up to 14 km, hence are own recruits. Here all young owls had been ringed systematically. In a peripheral area of about 40 km, from where seven more yearlings originated, there was no systematic ringing. So clearly more yearlings could have originated from this distance. But as they were not ringed, no numbers for their moving distances do exist. The considerably high mean value results from the fact, that four birds came from distances >100 km, one even from more than 300 km.

Different from the values of origin for recruits, those for the birds which had moved inside the study area are of homogenous quality. (Immigrants which had bred outside did not exist.) Here both sexes (N=12 each) could be studied separately. It is visible that the ♂ moved less far (mean 4,8 km) than the ♀ (mean 6,2 km). BAUDVIN (1986) who did not separate for the sexes found moving distances in the same magnitude.

4.3.1 Site fidelity of the breeders

Earlier authors (SCHNEIDER 1928, SCHIFFERLI 1957, SCHÖNFELD & GIRBIG 1975, SCHÖNFELD et al. 1977, KAUS 1977, BAUDVIN 1986) unanimously found much more often a longer fidelity to the breeding site in the ♀ than in the ♂. The present study indeed shows a contrary picture: More ♂ than ♀ originate from the own population (tab. 4) and more ♂ than ♀ stay at the same breeding site from one year to the next (tabs. 5,6). Accordingly the mean time for staying at the same breeding site is greater in the ♂ than in the ♀ (chap. 3.4.1). Certainly the difference to the earlier authors which exclusively studied free breeding owls is caused by the fact that here it is much more difficult to catch the ♂ than the ♀. So the catching numbers for this sex are much smaller. In BAUDVIN (1986) we read: „Et si la capture est si aléatoire, que dire de la recapture? » [And if capture is already so hazardous, what should I say about recapture?] In contrast, the population studied here is a mere box population with mean yearly catching rates of 77% in the ♂ and 83% in the ♀. Correspondingly the estimation of site fidelity is much surer.

4.3.2 Age of the breeders

In chapter 3.2 we stated that in worse years the mean age of the breeders was about one year higher than in the better ones. Three explanation for this difference seem possible: Especially younger owls could have suspended breeding or yearlings could have made their first brood not before their 3rd year of life. In the study population there really were observed 23 individuals (13 ♂ and 10 ♀) which had not been observed for 1-4 years as breeders, two ♀ even 1-3 times. These years of suspension however were in no connection with the quality of the respective years. As a second explanation there is the possibility that especially younger birds had left the study area and bred elsewhere. There are no proofs. The most likely explanation

seems to be that those years were preceded by an extraordinary mortality of younger owls.

It was generally stated (fig. 16) that among the breeders age distribution differs between the sexes. The proportion of yearlings in the ♂ is distinctly lower than that in the ♀. In the middle aged and in the aged breeders this portion correspondingly is higher. The nearby presumption (SCHÖNFELD 1977) the ♂ would be mature not before their third year of life repeatedly has been refuted (MEBS 1987, GLUTZ VON BLOTZHEIM & BAUER 1994, KNIPRATH et al. 1999). But it also seems possible that the yearling ♂ would have a lesser chance to find a breeding site with sufficient prey abundance in its surroundings. Consequently they would not find a mate. This possibility might become evident by finding a certain number of ♂ which were breeders not before their third year. The numbers in this study do not support this supposition: Twenty of the 29 recruits known by age (16 immigrants, 13 local ones) were yearlings and of the 9 older ones 5 were ♂ and 4 ♀. Hence there was no distinct difference.

As further reasons we could assume that there was a biased sex ratio already in the eggs or that ♂ would suffer a greater mortality until they breed for the first time. At least a non biased sex ratio in these developmental stages can be assumed as ROULIN et al. (2001) found a non biased ratio in the nestlings.

To reach a ♀ biased sex ratio after the first year an increased mortality of the ♂ could be demanded. Exactly this was deduced by ROULIN (1996) from the catching numbers in his study area. MASSEMIN et al. (1998) stated that the traffic victims were ♀ biased, in the younger birds as well as in the older ones. Similar influences can be assumed in the present study area.

4.3.3 Mate choice

At the beginning of every breeding season all recruits and the widowed birds are confronted with the task to find a mate. Though it seems possible that pair formation already happens in late winter (ROULIN 1998) for simplicity reasons we here assume a standard date immediately before the breeding season. As long as no winter controls have been realized we only can recognize by the later breeders who had been at disposal. Following table 7 the respective age groups (yearlings, middle old, old) at mating

meet candidates which preferably follow hazard as we saw in the offer in figure 16: Yearlings preferably find older mates whereas middle old and old ones meet candidates being younger than themselves and at a time being clearly younger than the preceding mates. Nevertheless all age groups seem to prefer mates of same age (tabs. 8,9).

How future mates meet seems to be clear from observations: The ♂ preferably seem to be sedentary (s. 4.3.1), occupy a breeding site and from there display to find a ♀ (EPPL 1985). The ♀ correspondingly are agile and seek. Until now obviously it has not been observed that a ♂ rejected a ♀ appearing. The inverse, namely that the ♀ continue seeking if they do not agree with anything connected with the ♂ they found, can well be imagined but has not been observed as well. This mechanism seems to offer little choice to the ♂, but very much to the ♀. Nevertheless ♂ as well as ♀ realize gains in partner quality when repairing, the ♂ preferably when staying, the ♀ when moving (tab. 8). That indeed seems to be understandable to the observer: The ♀ certainly know their neighbours in the vicinity and if widowed ♀ first look at sites where they remember a suitable candidate. Then it would be a mistake if the ♂ would move. Vice versa it would be fairly disadvantageous if a widow would stay at her breeding site: The ♂ do not seek. When repairing ♂ as well as ♀ do find a new mate of higher quality (life production, s. tab. 10). Principally that is not logic but explainable: By demographic reasons middle old and old breeders if re-mating often find yearlings as new mates (tab. 7). These do have the greater breeding success (tabs. 11-13). The quality of a breeder may be measured by different methods: as life production, as mean success per brood, or even as success in the single phases of the broods. Different to many other bird species (CURIO 1983, BLACK 1996, ENNS et al. 1996:360) barn owl yearlings breed at least as successful as older birds (disregarding old ♀) (see chapter 3.5.2.1). This holds true for owls breeding only once in their life as well as for the first brood of multiple breeders in comparison to their later broods. This greater success of the yearlings exclusively is based on their greater egg production. And here the contribution of the ♂ obviously is greater than that of the ♀ (fig. 39). The performance of both sexes as measured in

fledglings then is much reduced in the middle old owls and increases again towards older age. But when regarding the success in the two following phases of the brood, i.e. incubation and raising the young, then the middle old breeders prove as the far most successful breeders and the yearlings as the most unsuccessful ones. This difference may have several reasons: Already the quality of eggs or sperms (and so the portion of fertilized eggs) may differ by the age groups. The ♀ may incubate differently consequent, turn over the eggs or brood. The ♂ perhaps are different in hunting skills or as lovers. Perhaps the yearling ♂ soon decrease their hunting efforts, the middle old ones in contrast remain consequent? Even under a productiveness viewpoint the middle old breeders are far on top: Starting with an equal number of eggs they realize much more fledglings than both of the other age groups. As production of eggs means costs, we could name the behaviour of the middle old breeders as especially economic. Of course it is unknown whether this success is based on increased effort during incubation and brooding. The cost reduction in egg production so could be equalised.

From the figures 50-53 we can deduce only first ideas what these differences in performance do mean for mate choice. At least it is certain that the yearling ♂ should be the most choosy ones for all ages. Despite all defaults during the incubating and brooding phases they “save” their advantage from egg production until the final success measured as fledglings. Perhaps from here the dominance of the combination of similar aged mates can be explained simply. The combination of yearlings is a successful option. As mate fidelity counts (s. chap. 3.5.2.2) barn owls mostly are faithful to their mate (s. tab. 6 and chapt. 3.4.3.2). So the combination of same aged birds is persisting over the years. After a depression during middle age it again will be successful in later years (fig. 53).

The better egg production of the yearlings and the better success counting fledglings as discussed here cannot be brought into harmony with the data in chapter 3.5.2.3. Following fig. 49 the older ♂ and ♀ start breeding earlier. At a time the earlier broods do have as well higher egg numbers (fig. 47) as the higher numbers of fledglings (fig. 48). In spite of the clear incline of the numbers during early summer the values of early spring no more are reached. This indeed

should be so as the yearlings being better in egg production begin breeding fairly later.

4.3.4 Mortality

Concerning mortality of the barn owl in continental Europe there are several studies (SCHIFFERLI 1957, SCHÖNFELD 1974, GLUTZ VON BLOTZHEIM & SCHWARZENBACH 1979, BAIRLEIN 1985, OELKE 1986, DE BRUIJN 1994, DE JONG 1995, MÁTICS 2000, ALTWEGG et al. 2003). There we find mortality rates for the single years of life. So during their first year of life between 64% (SCHIFFERLI 1975) and 71,8% (BAIRLEIN 1985) die. Thereafter mortality decreases over 50% (DE BRUIJN 1994) to 63% (BAIRLEIN 1985) in their second year to an average of 39% (SCHIFFERLI 1957) and 48% resp. (DE BRUIJN 1994) during later years. The values found here (59% for the first, 43% for the second, and 39% for later ones after tab. 14) in the first two years clearly are beyond the values in the literature, later they are in the range of these. In part the difference may result from the fact that the authors define “first year” very differently. The distribution of the losses of juvenile birds in the autumn and winter months as shown in figure 58 (predominant losses January – February) is very similar to that given by BAIRLEIN (1985) and also to that which SAUTER (1956) shows for the winter 1952/53. Indeed they are totally different from those of DE BRUIJN (1994) for two populations in the Netherlands and those of MÁTICS (2000) for Hungarian juvenile birds. The two latter authors found highest losses during the autumn months until November, but decreasing values thereafter. High losses in the months from October to January were found by TAYLOR (1994) for Scotland.

4.4 Density dependence

Following TAYLOR (1994) also in the barn owl we should expect a density dependence of the success numbers (eggs, hatchlings, fledglings). However, effects of that kind hitherto could not be demonstrated because of the prey dependant heavy oscillations in the owl populations (TAYLOR). From the figures 33 and 34 we could deduce a density dependence of the breeding success. But as here the number of broods per village means the sum over all years of the study, this is not possible. The only certain measure for density is the sum of broods per year. These values were compared to mean success values of the single years. Neither the egg number (fig. 35) nor the mean number of

hatchlings nor fledglings (both without figs.) were density dependent, hence in years with few breeding pairs not differing from those with many ones. As the number of breeding pairs is depending on prey density it could be deduced that the mean success values were independent from prey density.

An eventual density dependence should have become visible as follows (fig. 35): With the numbers of breeding pairs (for increasing prey abundance) the egg numbers should have increased from the minimum to a medium level as well. Only if this increase was at least lowered with higher numbers of breeding pairs one could therein recognize a density effect. A possible explanation could be: During inclining and during highest breeding pair densities the number of breeding pairs possible from prey abundance never is reached. The barn owls by far cannot reproduce as fast as rodents. Even if they could, the low number of boxes in the study area would have been limiting long before any density effect. (similarly Taylor 1994: 229: "Therefore it is possible that the availability of nest sites in conjunction with prey abundance serves to limit the maximum density of owls in any area. This limitation may only come into effect periodically following prolonged periods of good food supplies.")

Acknowledgements

I wish to thank Dr. Reinhard Altmüller for rendering his data. Dr. Beatrix Wuntke, Dr. Johan de Jong and especially Hubertus Illner kindly and carefully read the manuscript. Many thanks for doing so.

Summary

Barn owl *Tyto alba*: dynamic and breeding success of a population in Lower Saxony, Germany

From 1972 to 1992 Dr. R. Altmüller and H. Könecke controlled breeding barn owls east of Celle and marked adults and nestlings. Data then collected now are analyzed under the following headings: Age and origin composition of the population, remaining and quality of breeders and pairs, the specific efficiencies of the age groups during breeding, influence of site, years, egg laying data, and demographic factors. Barn owls of both sexes do not occupy breeding sites by hazard but choose. At least yearlings show a preference for same age partners. As mate fidelity generally holds true this higher proportion of same age mates remains stable during consecutive years. Yearlings perform at least as successful as older breeders. This success is based on their particularly high egg production. Here the influence of the ♂ is greater than that of the ♀. The middle aged breeders

are by far the most successful ones during incubation and brooding. Two different life strategies seem to be possible: 1. "put all one's eggs in one basket" or 2. to count for a career as breeder of several years. During the study period mean egg laying date was advanced near to one day p.a.. Now indication was found for any density dependence of breeding success.

5. Literatur

- ALTMÜLLER, R. (1976): Schachtelbrut eines Schleiereulen-Weibchens (*Tyto alba*). Vogelkundl. Ber. Nieders. 1: 9-10
- ALTMÜLLER, R. (1980): Eine Methode zum Fang von Schleiereulen. Die Vogelwarte 30: 333-334
- ALTMÜLLER, R. (1981): Die Schleiereule, ein Kulturfolger. in: 100 Jahre Hannoverscher Vogelschutzver.: 39-40. Hannover
- BAUDVIN, H. (1986): La reproduction de la Chouette effraie (*Tyto alba*). Le Jean le Blanc 25: 1-125
- BEGON, M., M. MORTIMER & D.J. THOMPSON 1996: Population Ecology. Blackwell Oxford, used German translation: Populationsökologie, Spektrum Heidelberg
- Black, J.M. (1996): Pair bonds and partnerships. 3-20 in: J.M. Black Ed.: Partnerships in birds, Oxford Univ. Press
- CRICK, H.Q.P., C. DUDLEY, D.E. GLUE & D.L. THOMSON (1997): UK birds are laying eggs earlier. Nature 388: 526
- Curio, E. (1983): Why do young birds reproduce less well? Ibis 125: 400-404
- DE BRUIJN, O. (1994): Population ecology and conservation of the barn owl *Tyto alba* in farmland habitats in Liemers and Achtenhoek (The Netherlands). Ardea 82: 1-109
- DE JONG, J. (1995): De kerkuil en andere in Nederland voorkomende uilen. Leeuwarden
- ENNS, B.J., S. CHOUDHURY & J.M. BLACK (1996): Mate fidelity and divorce in monogamous birds. 344-385 in: J.M. Black Ed.: Partnerships in birds, Oxford Univ. Press
- EPPLE, W. (1985): Ethologische Anpassung im Fortpflanzungssystem der Schleiereule (*Tyto alba*). Ökol. der Vögel 7: 1-95
- GLUTZ VON BLOTZHEIM, U.N. & K.M. BAUER (1994): Handbuch der Vögel Mitteleuropas 9, 2. Aufl. Aula Wiesbaden
- KANIA, W. (1994): Breeding phenology of *Parus major* in Poland, 1931-1993: Data from ringing schedules and nestling aging method. J. Orn. 135 (spezial issue): 11
- KAUS, D. (1977): Zur Populationsdynamik, Ökologie und Brutbiologie der Schleiereule in Franken. Anz. Ornith. Ges. Bayern 16: 18-44
- KNIPRATH, E., R. ALTMÜLLER, H. SEELER & S. STIER (1999): Zum Zeitpunkt der Brutreife mitteleuropäischer Schleiereulen (*Tyto alba guttata*). Vogelwarte 40: 145-146 [for English translation see www.kniprath-barnowl.de]
- KNIPRATH, E., B. WUNTKE, H. SEELER & R. ALTMÜLLER (2007): Verfrühung des Legebeginns bei der Schleiereule *Tyto alba*. Vogelwarte: in press [for English translation see www.kniprath-barn-owl.de]
- KOOIKER, G. (2005): Vögel und Klimaerwärmung: 28-jährige phänologische Beobachtungen in und um Osnabrück von 1976 bis 2004. Vogelkd. Ber. Niedersachs. 37: 99-111
- LUDWICHOWSKY, I. (1997): Langfristige Trends bei Flügellänge, Körpermasse und brutbiologischen Parametern erstbrütender Weibchen eines norddeutschen Bestandes der Schellente. Vogelwarte 39: 103-116
- MCCLEERY, R.H. & C.M. PERRINS (1998):.....temperature and egg-laying trends. Nature 391: 30-31
- MEBS, T. (1987): Eulen und Käuze. Frankh Stuttgart, 6. Aufl.
- OELKE, H. (1986): Schleiereule in: ZANG & HECKENROTH, Die Vögel Niedersachsens und des Landes Bremen. Naturschutz & Landschaftspflege in Niedersachsen; special series B, vol. 2.7: 58-64
- ROULIN, A. (1996): Balz und Paarbildungserfolg bei der Schleiereule *Tyto alba*. Orn. Beob. 93: 184-189
- ROULIN, A. (1997): Philopatrie chez la Chouette effraie *Tyto alba*. Nos Oiseaux 44: 55-56
- ROULIN, A. (1998): Formation des couples en hiver chez l'Effraie des clochers *Tyto alba* en Suisse. Nos Oiseaux 45: 83-89
- SAUTER, U. (1956) : Beiträge zur Ökologie der Schleiereule (*Tyto alba*) nach den Ringfunden. Vogelwarte 18: 109-151
- SCHIFFERLI, A. (1957): Alter und Sterblichkeit beim Waldkauz (*Strix aluco*) und der Schleiereule (*Tyto alba*) in der Schweiz. Orn. Beob. 54: 50-56
- SCHNEIDER, B. & W. SCHNEIDER (1928): Beiträge zur Biologie der Schleiereule. J. Ornithol. 76:412-419
- SCHÖNFELD, M. (1974): Ringfundauswertungen der 1964-1972 in der DDR beringten Schleiereulen. Jber. Vogelwarte Hiddensee 4: 90-122
- SCHÖNFELD, M. & G. GIRBIG (1975): Beiträge zur Brutbiologie der Schleiereule, *Tyto alba*, unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte. Hercynia N.F. Leipzig 12: 257-319
- SCHÖNFELD, M., G. GIRBIG & H. STURM (1977): Beiträge zur Populationsdynamik der

- Schleiereule, *Tyto alba*. Hercynia N.F.
Leipzig 14: 303-351
- SHAWYER, C. (1998): The barn owl. Arlequin,
Chelmsford
- TAYLOR, I.R. (1994): Barn Owls. Predator - prey
relationships and conservation. Cambridge
Univ. Press
- WINKEL, W. (2002): Sind Singvögel Anzeiger
von Umwelt- und Klimaveränderungen?
Langzeittrends bei Meisen und anderen
Kleinhöhlenbrütern im Braunschweiger
Raum. Milvus 21: 1-12
- WINKEL, W. & H. HUDDE (1997): Long term
trends in reproductive traits of tits (*Parus
major*, *Parus caeruleus*) and Pied
Flycatchers (*Ficedula hypoleuca*). J. Avian
Biol. 28: 187-189