

Barn Owl *Tyto alba*: Characteristics and breeding success of a second (meta-) population in Lower Saxony¹.

KNIPRATH E, STIER-KNIPRATH S

Content

- 1 Introduction
- 2 Material and Methods
- 3 Results
 - 3.1 Breeding localities
 - 3.1.1 Distribution, altitude
 - 3.1.2 Rank of the villages by number of broods
 - 3.1.3 Egg-number and number of fledglings in relation to rank of the breeding locality
 - 3.1.4 Locality of origin and rank of the own breeding locality
 - 3.1.5 Hatching date and rank of the own breeding locality
 - 3.2 Brood years
 - 3.2.1 Population oscillation
 - 3.2.2 Breeding success
 - 3.2.3 Age of breeders by years
 - 3.2.4 Laying date
 - 3.2.5 Storage of prey
 - 3.2.6 Non-breeders
 - 3.2.7 Immigrants
 - 3.2.8 General characterization of the years
 - 3.3 Broods
 - Laying date*
 - Clutch size*
 - Multiple broods*
 - 3.4 Breeders
 - 3.4.1 Origin of breeders
 - 3.4.2 Abode of breeders
 - 3.4.3 Laying date and age
 - 3.4.4 Breeding success and age
 - 3.4.5 Breeding success and laying date
 - 3.4.6 Pairs
 - Pair formation*
 - Success of pairs*
 - Breeding success and faithfulness*
- 4 Discussion
 - 4.1 Breeding localities and sites
 - 4.2 Yearly oscillations of the success values
 - 4.3 The breeders
 - Origin*

1 Translation of: Schleiereule *Tyto alba*: Eigenschaften und Bruterfolg einer zweiten niedersächsischen (Meta-) Population. Eulen-Rundblick 64: 43-65

Age

4.4 Correlation of the phonologic date of the broods

4.5 Pairs

5 Summary

1 Introduction

The results origination from the ringing activities of R. Altmüller in the years 1972 – 1992 had lead to many kinds of new knowledge belonging to the breeding biology of the Barn Owl, especially the role of the individuals (KNIPRATH 2007). The present study indeed comprises fewer years, but the number of nest boxes threefold exceeds the need of the Barn Owls. Onto that a bad rodent-year 2009 and two following snow-winters had reduced the population to a minimum. The now following years so presumably will serve to the study of the regeneration of the population. The field work itself will be continued unchanged. Here we will depict the results of our ringing activities in the northern county of Northeim, as far as they concern the properties of the years, the breeding localities, and the properties and qualities of the breeders.

2 Material and methods

The study area comprises the northern half of the southern-Lower-Saxonian county Northeim (the areas of the communities Einbeck, Dassel, Bad Gandersheim, Kreiensen, and Kalefeld) with altogether 518.66 km² (county-info), geographic centre near Einbeck (9.87 East, 51.82 North). The area is composed by several smaller depressions (Ilmesenke, 100-170 m [altitude]; Heberbörde, 160-190 m; Harzbörde, 140-160 m) and river valleys (Leine, Gande, Ilme, Aue) between ridges (200 – 400 m). The depressions and valleys are intensely used for agriculture with elevation of cereals (maize increasing), rape, and sugar-beet (decreasing). As in other regions as well, the fields were and still are growing, what lead and leads to the loss of margin-structures. Figure 1 gives an impression (Leine-retention basin). The ridges mostly are wooded.



Figure 1: View from the quarry Vogelbeck in direction West on the Leine-valley and the Ilme-depression

Most human settlements (without separated farms: n=104) preferably are villages with a small, dense centre. Where vast new settlements (not habitable for Barn Owls and without nest boxes) had been constructed, these nearly never totally surround this centre. For the owls mostly there is a short way from the breeding site in the old centre to open landscape. In the greater towns (Einbeck, Bad Gandersheim, Dassel) centrally installed boxes never have been used, more laterally ones only rarely. There are eleven isolated farms with boxes. Three of the six boxes in isolated barns were used once, one repeatedly and one never. The altitude of the villages is shown in figure 2.

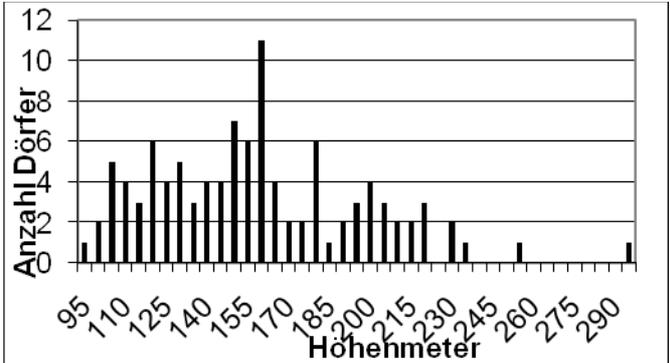


Figure 2: The altitudes of settlements (n=104)

We have a nearly exclusive breeding-box-population. The total of boxes oscillated around 310, with a mean density of about three boxes per settlement. The boxes had been posted during the 70ies by a few private people and mostly by HORST WEITER, Göttingen, as a team-action together with the then “Deutscher Bund für Vogelschutz” (DBV), today “NABU”, and of the county Northeim. HORST WEITER has done the greatest part of the logistic. Losses of boxes and additions to the total didn't alter the general distribution. Only two settlements until today don't have any nest box. The first one is situated in a narrow valley and mostly surrounded by wood; the second one only consists of newer dwelling houses around a factory, situated at a wood-border.

All boxes are positioned inside of buildings, about 84% in barns and stables, 9% in churches (towers and loft of the nave), as these buildings generally are sufficiently high and onto that do have high outer walls (safety against marten). These buildings nearly all belong to the old village centres. That means, the distance between the boxes inside a village not exceeding some hundred metres. Occasionally there are two boxes in one farm or even immediately side to side. All boxes are fixed to the inner side of an outer wall of the building and for safety against martens for the owls only accessible through an opening in the wall (Figs. 3, 4). Boxes at walls not smooth or at such consisting only of beams, laths, tiles, or corrugated sheets often do have an entrance-tunnel of 10-30 cm. These as well so are properly marten safe.



Figure 3: Entrance of a Barn Owl nest box with tunnel, seen from outside the building



Figure 4: Barn Owl nest box inside a building with a wall covered by tiles

The nest boxes are mostly identical being 100x60x60 cm. Peculiarities of the construction have been adopted from ALTMÜLLER (1980). Alterations only concern peculiarities for trapping the adult birds. The boxes contain a soil-covering of shaving, about 2 cm thick. They are cleaned after the brood of owls (but not after a brood of Kestrels) and again fitted with shaving.

The study began with the breeding period 1996, a special peak of the local population. Here we analyse the years until 2010 (incl.), i.e. 15 years. Data from a learning period during the years 1990-1995 in a part of the area occasionally are used as well with special indication. In part as well data from the southern half of the county, where the not consequent ringing had begun in 2005, were used.

Just at the first control of each year we tried to catch the (present) adult bird(s) and ringed them. (The rings were furnished by courtesy of the Vogelwarte Helgoland.) To do that, the box, as often as possible, was closed from the exterior by a plug of hard foam, fixed to a long stake. So the adult bird(s) could be met back into the box after ringing or control and regularly stayed therein. So eggs or pulli eventually present didn't remain alone to long and could not cool thoroughly because the ♀ was absent. The ♂, often not being present at this first control, later were trapped by a then installed removable flap with automatic release by trip-wire (after ALTMÜLLER 1980), after the young already had hatched. During this trapping the always present ♀ together with her brood was fixed within the box under a wire-box. So the catch flap only could be released by ♂ entering the box with prey. The young could not suffer any harm as their mother all the time was present. She again remained totally relaxed, as she indeed was with her brood.

If at this first control eggs and also hatched young were found, so at one hand the clutch size was known and on the other hand egg laying could be calculated (the laying interval was assumed to be two days and the incubation time generally 30 days). If only eggs were found, later a second control was performed to have the final clutch-size and the laying date calculated by the calculated age of the young. If at the first control we already found young, we counted their number, adding eventually not

hatched eggs, as clutch-size. This latter one occasionally could be underestimated in these cases, if single young had died shortly after hatching without leaving a trace. (As to the consumption of dead young see KNIPRATH & STIER-KNIPRATH 2010). Single misplaced eggs were counted as brood.

The methods of analysing and as well die presentation of the results, including the structure of the paper, mostly are the same as in an earlier study (KNIPRATH 2007).

Graphs were produced by MS EXCEL. Tests of significance for differences between means were performed with ANOVA (in MS EXCEL) and the significance level was fixed at $P < 0.05$.

3 Results

3.1 Breeding localities

3.1.1 Distribution, altitude

As is to be expected, the distribution of the altogether 785 (those from 1990 – 1995 included here) broods in the study area were found distributed very irregularly (fig. 5). Gravity centres are the three depressions mentioned above and forth one SW of the village Kalefeld. The decline of the numbers of broods with the altitude becomes apparent in fig. 6. This correlation could be a fictitious one as already the number of villages itself is altitude-dependent (fig. 7). This supposition is not confirmed, if the number of broods per village is depicted against the numbers of villages per altitude interval (fig. 8). Even within the indeed here small difference of altitude of 250 m the owl density is altitude-dependent. During the study interval in 19 of the 102 localities with nest boxes there were no broods at all. These localities are found in all altitudes (fig. 9). The altitude apparently is not the important factor, if villages totally are avoided.

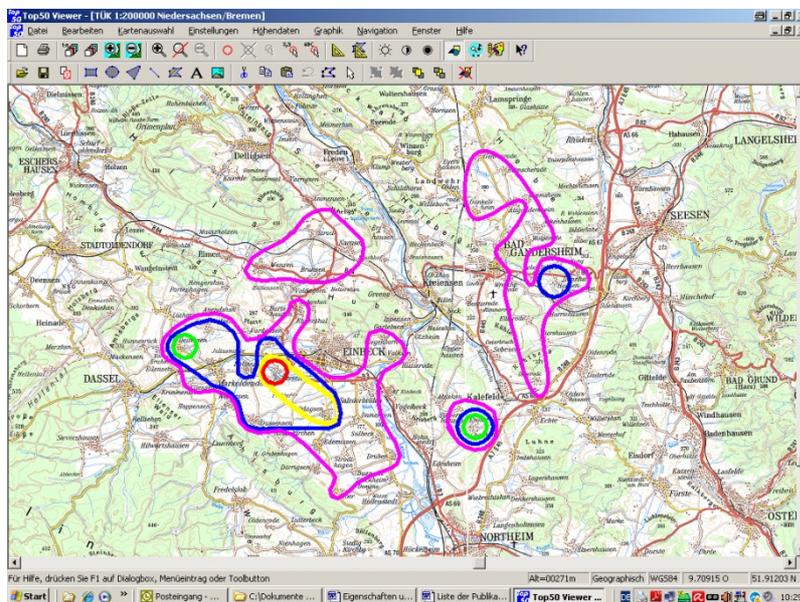


Figure 5: The distribution of the broods among the villages, given as isoclines, which include localities with at least 5 (violet), 15 (green), 20 (yellow), and 25 broods (red). Data from table 1.

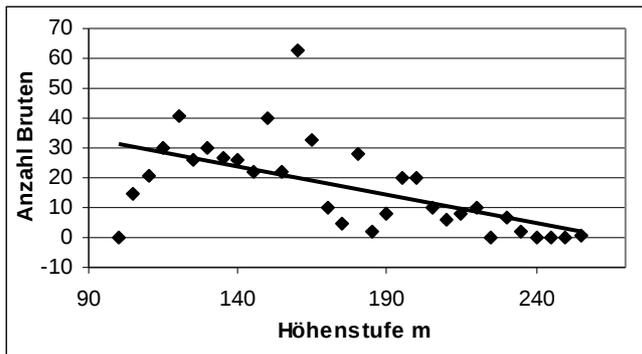


Figure 6: Altitude-dependence of the brood numbers (n=785)

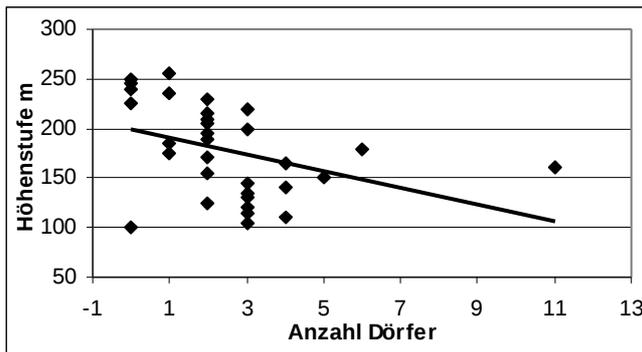


Figure 7: Number of villages per altitude (n=104)

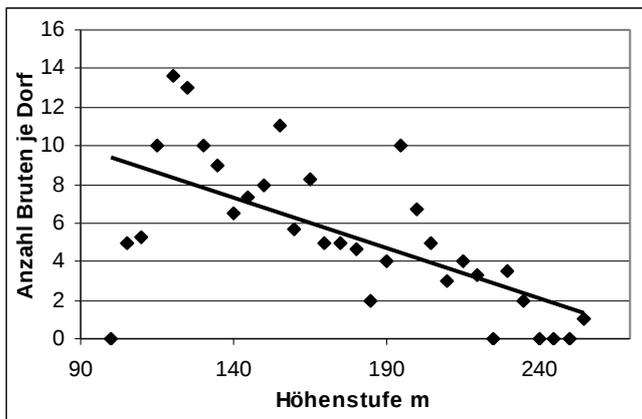


Figure 8: Relative number of broods (to number of villages) per altitude

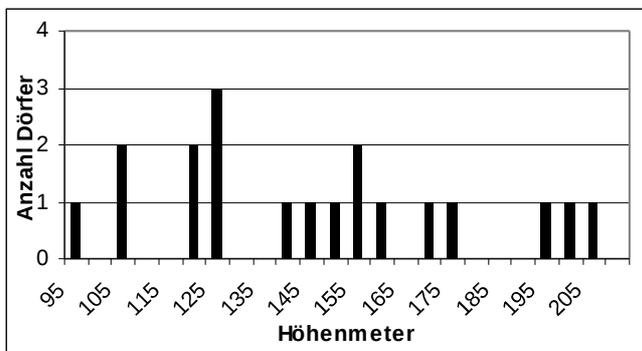


Figure 9: Altitude of villages without broods

As well as the villages, the boxes not have been used with a uniform frequency. The service life extended from zero (never used: 33.6% of the boxes) over once (47.5%) up to 14 times (one box). Herein replaced boxes or moved ones each time are counted as individual boxes. In the 9% boxes hanging in churches, 6.1% of the broods took place. The special altitude above ground of these boxes obviously has no special force of attraction to the owls.

Free broods mostly are unknown. Among the broods found hitherto there were only three, one of these unsuccessful, of the second one the adult birds as well as the young, and of a third one, probably the second brood of a known pair, a part of the young could be ringed. There were four cases of strong brood suspicion, two of these in an inaccessible box, and twice as well outside a box. We did not systematically seek for those broods but looked for all cases of suspicion indicated.

3.1.2 Rank of the villages by number of broods

We ranked the villages following the number of first broods which had taken place there 1996-2010 (n=426). Table 1 lists the first 10 ranks (22 villages). The special rank of each village is taken as a preliminary measure of its quality and/or solely of its popularity.

Dorfname	Anzahl Bruten	Rang
Hullersen	26	1
Odagsen	22	2
Eboldshausen	15	3
Deitersen	15	3
Markoldendorf	13	4
Kohnsen	12	5
Dassensen	12	5
Amelsen	11	6
Hachenhausen	10	7
Drüber	9	8
Edemissen	9	8
Gremshheim	9	8
Dannhausen	9	8
Salzderhelden	8	9
Volksen	8	9
Einbeck	8	9
Ackenhausen	8	9
Dankelsheim	8	9
Iber	8	9
Stroit	8	9
Kuventhal	7	10
Buensen	7	10

Table 1: Rank of the first 22 villages following the number of first broods as documented there during the study interval (n=426)

In the four villages of the first three ranks in total 18.3% of all first broods took place, in the four worst years (with <20 broods: 1997, 2002, 2006, 2009, 2010) indeed 32%. Here as well we found nearly all cases of simultaneous more than one first broods of a year: Odagsen (peak number: 5), Hullersen (3), and Markoldendorf (3).

We conclude from the differing frequency of using the boxes as well as the villages that this latter one is not hazardous but originates in a choice by the owls. This choice happens when yearlings, immigrants or movers (again) settle. These three possibilities will be analyzed separately. We here use only the first broods within the years.

First we ask: Does the age of the breeders differ depending on the rank of the village? The answer is, as can be seen in figure 10, for both sexes a definite yes. For this figure the immigrants were classified as yearlings. A higher mean age may be reached by two ways: At some places the owls become older and/or they stay longer there or the mover there with increasing age. These two possibilities will be tested. The generally older age of the ♀, as it appears here, again will be addressed later (3.4 breeders).

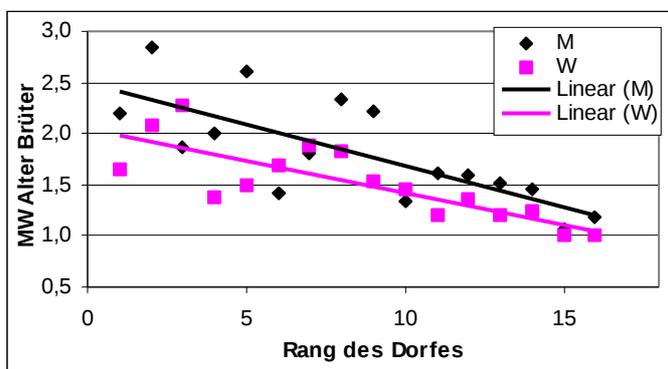


Figure 10: The mean age of the breeders in relation to the rank of the village following table 1 (σ : n = 361; ♀: n = 377)

25 of the 35 pairs, which had been faithful from year A to year B, stayed in the same box, nine more in the village. The only pair having moved to another village has evaded building operations. Faithful pairs thus stay at the breeding site or in its nearer surroundings. The anterior breeding sites of these 35 had a rank-median of 8, that of the pairs, which had been faithful to the box, of 4. We there from deduce that the site faithfulness of the faithful pairs contributes to the higher rank of a breeding site.

Among the 69 σ (not including the faithful ones), which had been found in a following year as breeder, 28 (40.6%) had stayed at the site, 41.6% had moved. Among the 52 ♀ 22 (42.3%) had stayed, 30 (57.7) moved. For these movers the rank-median of the original site for both sexes was at 11, that one moved to at 9. So, many of the owls had used moving to occupy a rather higher-ranked site. For the σ we found the same rank of the new site as for the pairs that had stayed: 8, for the ♀ of 6.5, i.e. a clearly better one. We see: Who already occupies a good breeding site, if possible stays there, the staying interval there is longer, the rank of the site increases. Who moves tries to occupy one of these sites. Also by that the rank of these sites increases.

Male own yearlings (n=58) for their first brood found a breeding locality with a rank-median of 11. For them we may assume that they mostly knew the quality of the offer. With this rank of their first breeding site they were less successful than the moving σ . Yearling, which had immigrated (σ : n=13), were clearly better with their

rank-median of 9 of their breeding site. Among the ♀ the own yearlings (n=36) were as successful as the immigrated ones (n=14), the breeding site of both had a rank-median of 9.

In the last category, the immigrants of unknown age, the ♂ (n = 135) with a rank-median of 11 were as (less) successful as the ♀ (n = 233) with the same rank-median and so less successful than the immigrated yearling with a rank-median of 9.

3.1.3 Egg-number and number of fledglings in relation to rank of the breeding locality

As a reason for the continued occupation of a breeding locality we could assume that here the prey offer mostly would be better than at other places. This as well could be visible in the egg number. Figure 11 demonstrates that there is no connection between the choice frequency of a locality and the mean egg number there. That still is true, if we compare only the villages of table 1 instead of using all.

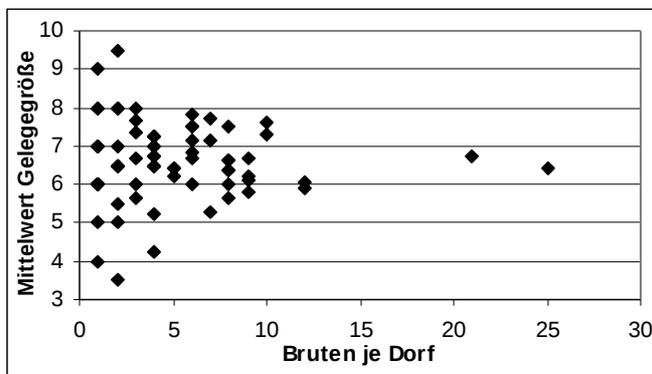


Figure 11: Mean clutch size in relation to the total number of the broods of the localities (all localities with broods; n=76)

Indeed, likewise the certainty of the prey offer also in less good years could be the reason for the preference of these localities. We could see that in the elevation success, i.e. the numbers of young fledged. Figure 12 with all villages makes recognize a feeble tendency to the villages with more broods. This one indeed mostly disappears, if only the villages of table 1 are compared (fig. 13). This tendency may have the reason that villages with a lesser rank mostly only are used in especially good years (with the then generally especially good elevation success).

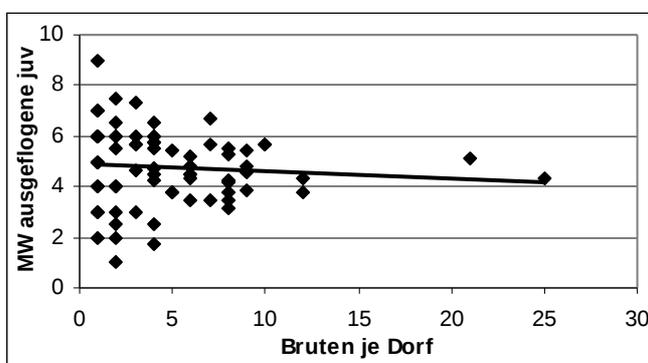


Figure 12: Mean number of fledglings in relation to the total number of broods of the localities (all villages with broods; n=76)

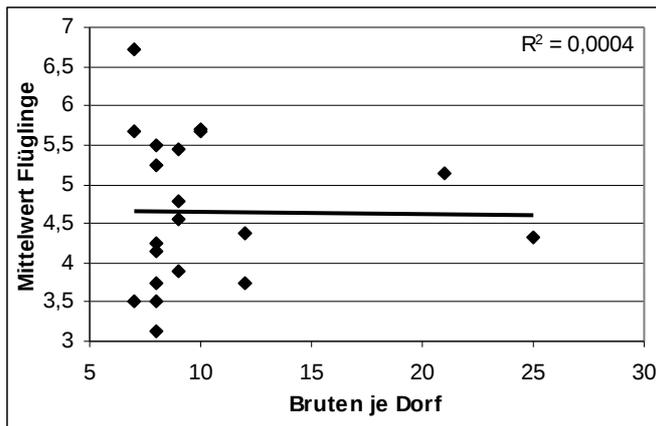


Figure 13: Mean number of fledglings in relation to the total number of broods of the localities in table 1

3.1.4 Locality of origin and rank of the own breeding locality

In direct connection with the success of the yearlings at occupying a breeding site of higher rank is the question, whether this success is depending of the rank of the family of origin. This latter one not can be deduced from the present material. A measure for it indeed could be the rank of the breeding site of the parents. The figures 14 & 15, alone by reason of the very strongly and rather even uniform variation of the values, make assume that this is not the case.

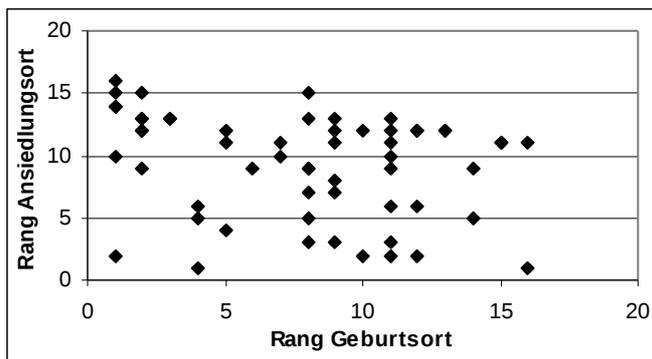


Figure 14: The settling success of male yearlings by the rank of their birth-site (all own recruits, included those of the preceding study; n=58)

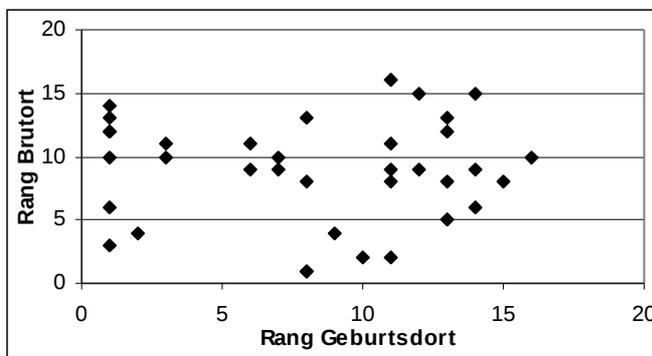


Figure 15: The settling success of female yearlings by the rank of their birth-site (all own recruits, included those of the preceding study; n=36)

Moreover it seemed possible that the recruits coming from higher ranked birth sites generally had a higher possibility to settle in the study area. Here we analysed only the σ as they occupy the breeding sites. It appeared (fig. 16) that there could be such an advantage (very low R^2).

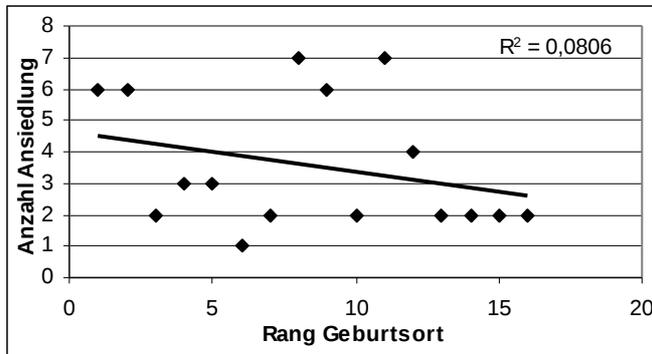


Figure 16: Numbers of settlings of own recruits (σ) in the study area by rank of the birth site (n=58)

3.1.5 Hatching date and rank of the own breeding locality

As well as owls, which had fledged earlier in the year, breed nearer to the birth site and generally more often reach breeding age (Kniprath 2012: 108), they as well could be more successful in occupying a higher ranked breeding site. For this, figure 17 gives no indication. We here merely recognize that the majority of the broods had been started during springtime, a smaller part in the second half of the year. When looking at these two groups separately there indeed a clear difference appears. For the spring time broods (fig. 18) there seems to appear a trend in the direction that those who had hatched earlier, preferably find a worse breeding site. We did not succeed in finding a reason for this. Surely there is no connection with the observation that about one third of the boxes had been occupied by kestrels. The situation for the late broods looks different (fig. 19). Here those with the earlier birth dates apparently occupied the better sites. They certainly had the better opportunity, as at the time of their egg laying all kestrels had left the boxes occupied by them during spring time and as well a greater part of the boxes hitherto occupied by Barn Owls now were free. This indeed fits much more for those young owls, which again later had started their broods.

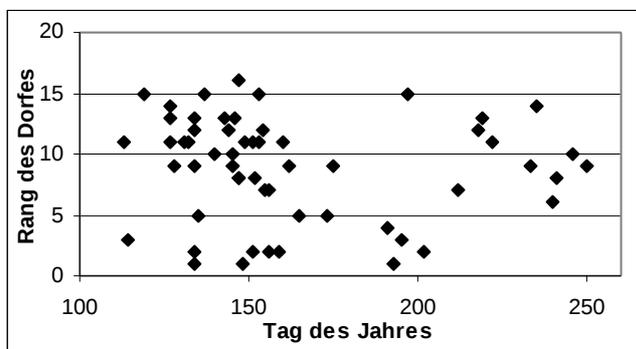


Figure 17: The correlation between the birth-date of the owls (σ only) and their success in occupying a box by rank of the village (n=57)

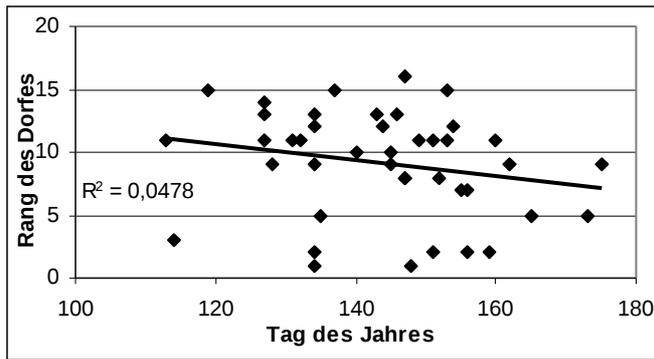


Figure 18: like fig. 17, bur only spring broods; n=42

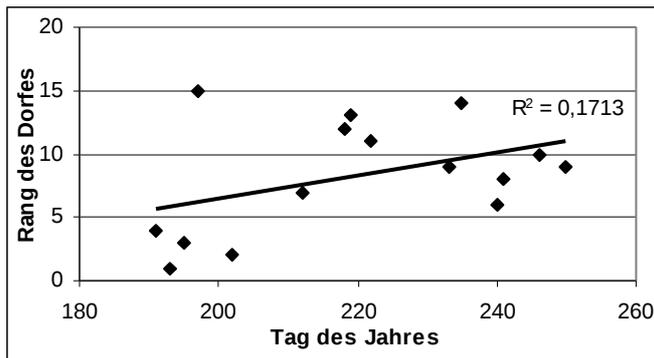


Figure 19: Like fig. 17, but only late broods; n=15

3.2 Brood years

3.2.1 Population oscillations

The known, sometimes violent, and by the prey offer caused from year to year oscillations of the numbers of broods (TAYLOR 1994) are also found here (fig. 20). Following this criterion the years 1996, 2001, and 2005 can be named especially good years. As the first year of the study has been an extraordinary good one and the last one indeed one of the worst ones, it seems unrealistic to derive from these numbers a trend of the population. Nevertheless it is interesting that the three peak years for themselves show an increase.

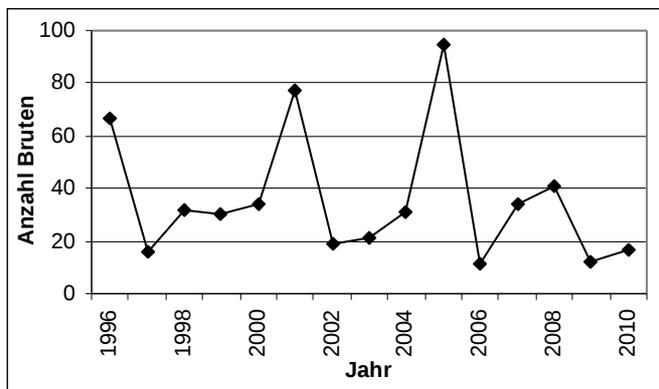


Figure 20: Numbers of all broods by years (n=537)

For a better understanding of the development of the population up to the year 1996, we here look at the data of the years before 1990 (fig. 21). These data originate from

a pre-study in a part area, the communities Bad Gandersheim, Kalefeld, and Kreiensen (239.83 km²: county info). There it becomes apparent that up to the year 1995 there was a rather gradual (with the usual jumps), but towards the year 1996 a furious increase of the brood numbers. In spite of the crash in the years 2009 and 2010 the trend line altogether shows a clear increase of the population. As in figure 20 the curve in the corresponding years including the pikes in the years 1996, 2001, and 2015 has a mostly parallel course, we assume that the development in the total study area in the years before the study was similar. If the aim of the study only had been to know the population development, the study of the part area would have been sufficient.

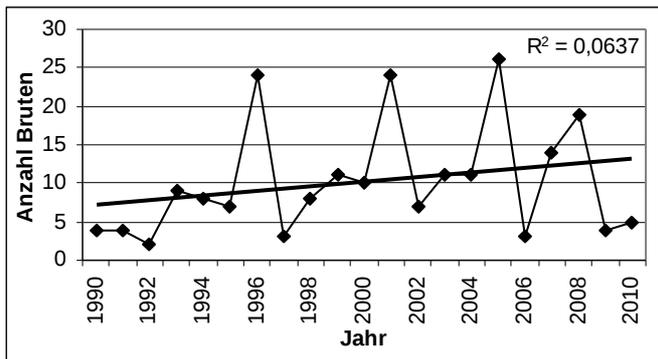


Figure 21: Total numbers of broods in a part area of 239.83 km² by years

3.2.2 Breeding success

If we indeed look at the breeding success of the owls (fig. 22), the years 2004, 2007, and 2010 appear as peak years with a mean of >7 eggs and >5 young fledged. The year 1999 was not so clear. So there is not a single correspondence with the judgement after brood numbers. It is noticeable that the values of the years 1996-2003 are close together and that greater oscillations only appear thereafter. The differences between these means are not significant (P=0.9).

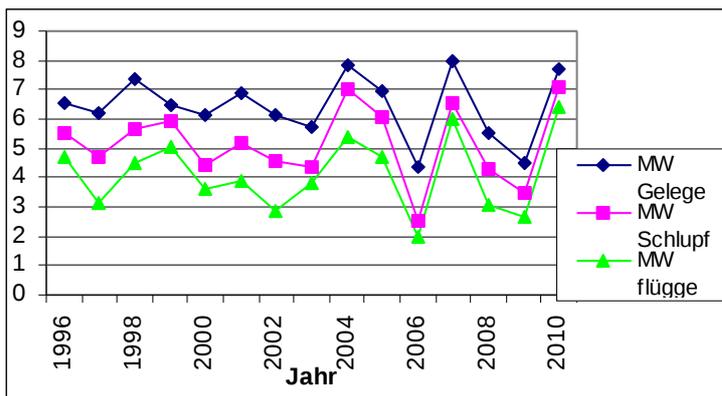


Figure 22: The breeding success in the years of the study

It seemed possible that the breeding success of the pairs would be influenced also by the density of the population (as brood numbers per year) in the study area. Figure 23 indeed demonstrates that there was no such influence.

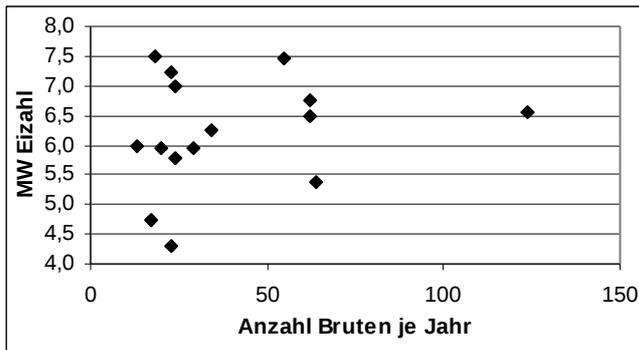


Figure 23: Mean egg number in relation to the number of broods (without second ones) per year (n=594)

More interesting than the numbers themselves are the changes during incubating and brooding, what here means losses. In figure 24 these are depicted in two steps: eggs not hatched and losses up fledging. The course of the two curves is totally different, in part even counter-rotating. Interestingly the course of the curves to a certain extent narrows, if we compare the relative values instead of the absolute ones (fig. 25). Table 2 shows the total means of losses for all values, table 2a only for the data used in figure 26. The small losses in the first broods may be due to the fact that these develop into the multiplication phase of the rodents.

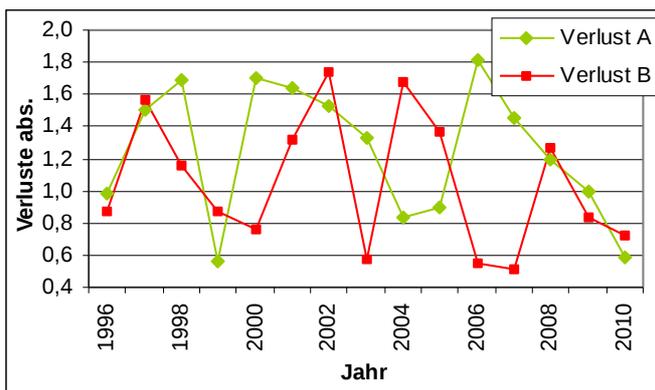


Figure 24: Absolute values of losses (means) of eggs during incubation (not fertilized or died) (loss A) and of pulli (loss B) (all broods)

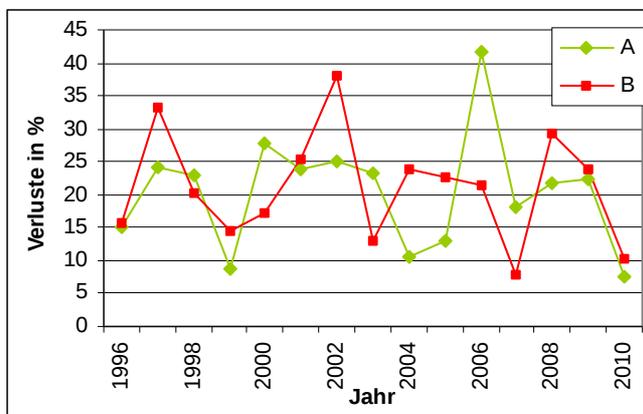


Figure 25: Relative losses (means) of eggs during incubation (not fertilized or died) (loss A) and of pulli (loss B) (all broods)

stage	mean	loss abs.	loss %
eggs	6,6		
hatch	5,4	1,2	20,2
fledge	4,3	1,1	23,1

Table 2: Total means of egg numbers, hatching numbers, and fledging numbers and the resp. Differences as number and as part in % against the preceding stage (all broods; n=520)

stage	mean	loss abs.	loss %
eggs	6,7		
hatch	5,9	0,8	11,9
fledge	4,9	1,0	17,0

Table 2a: Total means of egg numbers, hatching numbers, and fledging numbers and the resp. Differences as number and as part in % against the preceding stage (first broods only for both parents; n=311)

The summarized breeding success as depending from clutch size shows an astonishing uniformity (fig. 26). Besides for egg numbers of >10, for which the n were <5, the numbers of hatchlings differ only slightly around 75%.

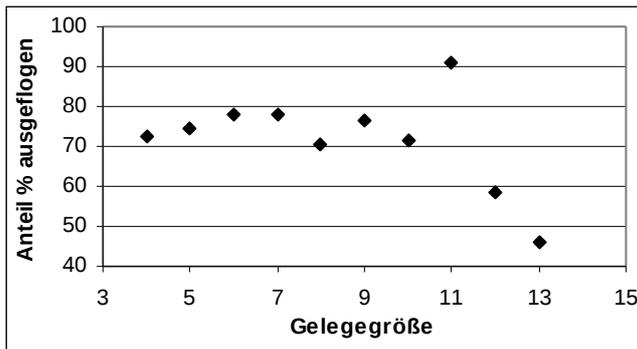


Figure 26: Fledging success of the broods as depending from clutch size; only first broods of both parents; n=322

3.2.3 Age of breeders by years

Besides the oscillating reproduction rate also the number of breeders changing from year to year may have their reasons in the mortality rate differing from year to year. The differing age of the breeders over the years might give an indication for that. The determination of the age of the birds for figure 27 could contain a systematic error: In 1995 for a lacking banding permission we had not ringed. So among the own recruits this cohort is lacking. The age values for the about four years (until 1999) therefore with diminishing extent are to high. In this figure it becomes evident that the alteration of the mean age over the years for both sexes clearly was different: During the first half of the study interval, the ♂ on average were older than the ♀. The only clear common feature is the very low value for the year 2006. The subject “age of the breeders” again will be stressed in chapter 3.4 “Breeders”.

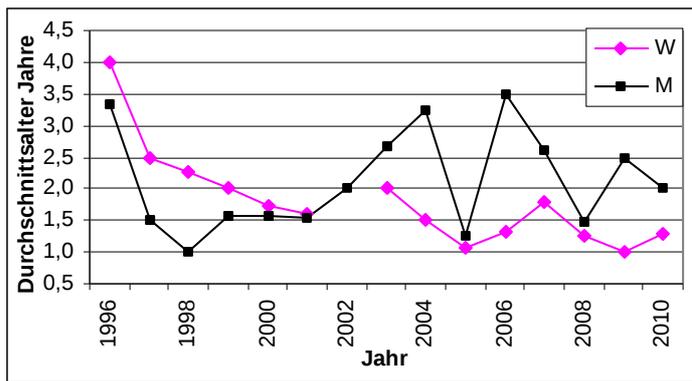


Figure 27: The mean age of the breeding birds (ringed as nestlings) by years (for the ♀ in 2002 there is no owl with exactly known age) (σ : n = 120; ♀: n = 69)

Likewise the age of the original immigrants was compared (fig. 28) assuming, they had been yearlings at their first brood in the study area. Both curves mostly are parallel. Indeed the σ mostly were slightly older than the ♀.

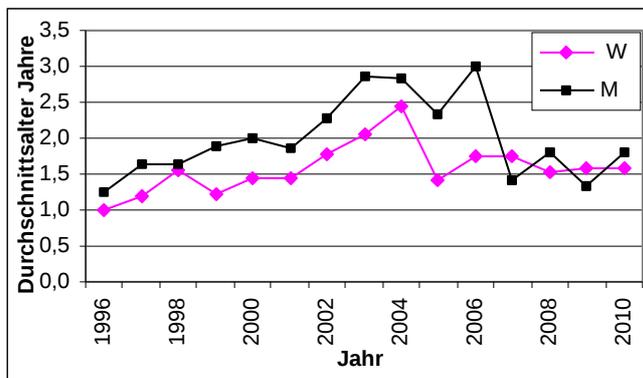


Figure 28: The mean age of the original immigrants, assuming that they had been yearlings at their first brood (σ : n = 289; ♀: n = 377)

3.2.4 Laying date

The laying date is a further characteristic oscillation from year to year. Figure 29 shows these oscillations for the medians. We directly see only little parallelism with the criteria of quality as already discussed: number of broods and breeding success (figs. 20, 22). An eventual trend of change of this date is not visible. (The means are nearly identical with the medians. So any deduction fits for these as well.) In figure 30 it becomes very clear that an early egg laying coincides with a higher density of the population. This correlation not at all is caused by the three extraordinary good years with >60 broods (red). If we eliminate these the correlation with density becomes clear (green). Both trend lines do have a R^2 of 0.2. Both values, number of breeding pairs and laying date obviously are depending on the prey availability during the respective preceding winter.

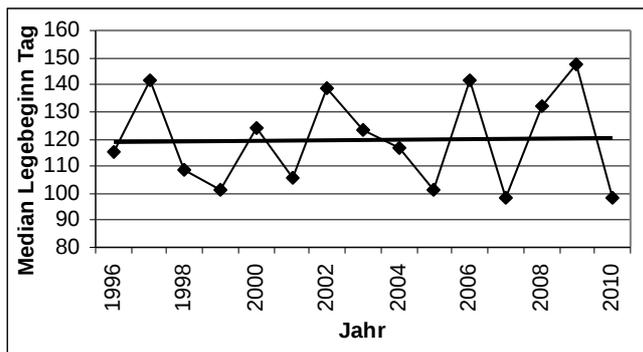


Figure 29: The oscillation of the median of the laying date by years (in days after onset of the year; day 100 corresponds to April 10, day 145 to Mai 25) (n=323)

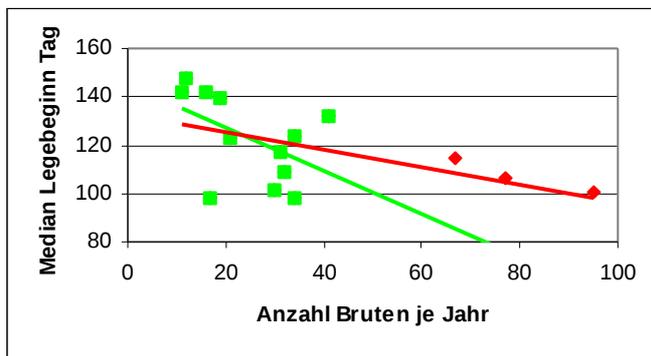


Figure 30: Correspondence between the numbers of broods of the year with the median of the laying date (in days after onset of the year): green + red: all values; green: without the three extreme years (red dots). (n=323)

3.2.5 Storage of prey

In Barn Owls storage of prey in differing quantities may be found in immediate neighbourhood of the brood (lastly analysed for quantity and function by ROULIN 2004). These numbers as well could contribute to the characterization of a brood-year. They do exist, beginning with the year 2000. These data not were collected with sufficient systematic. In addition, the controls happened at differing daytimes. As is known, the stored prey diminishes in the course of the day by consumption. This mistake indeed is not year-depending.

We speak of altogether 366 controls, at which 1.135 prey items were found. Field voles (*Microtus arvalis*) contributed 746 items (65.7%). The remaining specimen mostly were long-tailed mice, mostly *Apodemus flavicollis*, in smaller numbers also *Arvicola terrestris* and *Talpa europaea*.

Here the numbers of prey items per control as well as the part of the field vole are of interest, as they both tell something about prey availability and by that about the quality of the respective year (fig. 31).

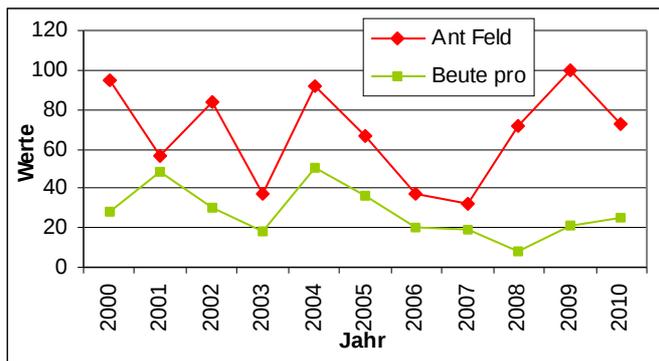


Figure 31: Number of prey items per control (“Beute pro”; n=366) (These values are presented in 10-fold magnification.) and the part of the field vole (%) by years

3.2.6 Non-breeders

For all owl species it is assumed that they certainly can suspend breeding. In the study area in the majority of the years single owls were controlled in the nest boxes, to which we could not adjoin a brood. Likewise there were birds, which have been controlled as well in the preceding as the following year, but not in the respective year. These eventual non-breeders altogether were faced indeed by the about three fold number of owls not controlled. Solely in the year 2006 there were 13 non-breeders opposite to 10 breeders not controlled and in the year 2010 four against two. So the year 2006 has been a classic non-breeder year. At the time also the success numbers were the smallest at all. For the success numbers the year 2010 has been extraordinary good. Why in the year 2010 an owl not should have bread remains uncertain. The numbers do not give any indication of the general validity of the postulate mentioned at the beginning.

Concerning the sex of the non-breeders, no statement can be given, as there was no certain characteristic to discriminate between them.

3.2.7 Immigrants

Firstly (fig. 32) it is noticeable that in all years the part of immigrants was higher for the ♀ than for the ♂. For the ♂ it scarcely oscillated, for the ♀ just more clearly. Here we see as well that the peak values of the breeding pair numbers 2001, 2005, and 2008 in a certain extent were caused by immigrants. (The values of 1996 not are to be considered, as we had not ringed in 1995.)

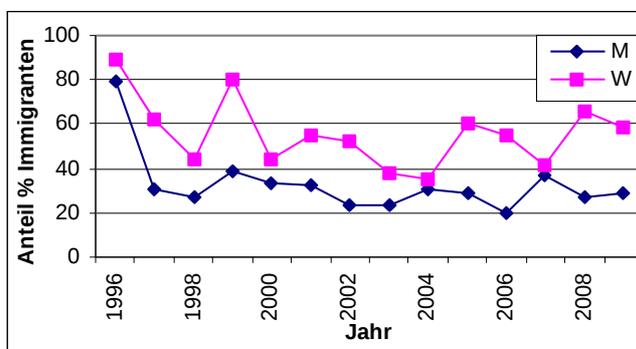


Figure 32: Part of immigrants by years (♂: n = 148; ♀: n = 305)

3.2.8 General characterization of the years

An earlier attempt (KNIPRATH 2007), to develop a measure of quality for the study years by the numeric characteristics as described hitherto, has been given up. From a combination of the figures 20-32 and the table 2 the following yearly trends of the development of the population may be derived and proving evidence been found. The indications concerning the micro rodent populations are given exclusively qualitatively after observations in the field.

At the beginning, in **1996**, we had a fairly high owl population but then average egg numbers. The losses during incubation as well as during brooding were scarcely below average. (Among the prey deposits in the boxes there was a very high portion of long-tailed mice, mostly *Apodemus*. The year 1995 has had a very rich harvest of beech-nuts. The *Microtus* population already during the summer 1995 strongly had declined.

The severe decline of broods to the year 1997 makes guess that the prey abundance (or the availability) clearly had decreased over winter. As the egg numbers had been beneath average and the part of eggs not hatched above average and the part of pulli deceased clearly above average, we may suggest that the prey offer did not become better over summer. (Late laying and one non-breeding pair, the prey delivered now mostly consisted of *Microtus*.)

Towards the breeding year **1998** the prey situation for the owls seemed to have bettered slightly: Laying date was very early and the number of broods moderately increased. The moderate increase of all success values and the average losses indicate that the micro rodent population already during the breeding period moderately increased. (increase of voles; second broods)

This normality endured **1999** and certainly also **2000**. As the number of broods increased very clearly toward the year **2001**, unless that the two preceding years would have been successful above average, we might look for a reason in a for the owls very favourable winter-half-year. At least for the ♀ immigration has played a certain role (fig. 32). The high breeding pair density was connected with suitable normal success values.

The very late egg laying and the crash of the brood numbers towards the year **2002** so must be attributed to a very clear decline in prey abundance over winter. Concerning this towards springtime there has been no change, what can be seen in the sub-average clutch sizes. The above average losses of pulli indicate that this situation lasted also over summer. (already during the preceding autumn lasting rainy times, which again appeared during spring time)

Towards the year **2003** the brood numbers did not alter. The egg numbers were clearly beneath average, the losses towards hatching then indeed only scarcely and those towards fledging clearly sub normal. Obviously the prey populations had recovered in the course of the late springtime. (warm summer; upward trend in the voles)

The winter towards the year **2004** obviously was favourable: The number of broods has been slightly increased afterwards and then the success values of the pairs increased above average. (good vole population, high number of second broods) These success numbers, together with an obviously favourable winter and, at least in the ♀, an increased number of immigrants (fig. 32), during the breeding season **2005** lead to a very early egg laying and the hitherto highest number of broods. An indeed already decreasing but still over average egg number together with rather low losses up to hatching and still normal losses of pulli were not sufficient to hinder the then following enormous crash. (greater number of own recruits and second broods;

highest bigyny numbers; strong losses in the second broods; several rain periods in September and October with decreasing vole numbers)

The year 2006 then brought the up to then lowest number of broods and again a very late egg laying. The egg number as well was as low as ever. And the losses up to hatching were the highest ones. At least the then normal losses of pulli allowed guess an upward tendency concerning the micro rodents. (late winter with snow and wetness during March with dead-recoveries ov Barn Owls; non breeders, as became visible in 2007)

The increase in rodent numbers obviously continued over winter and also the availability of prey remained good. In the year **2007** then the brood numbers again were slightly increased and egg laying very early. The egg number was at the peak level of the year 2004. In addition the losses up to hatching were below and those up to fledging clearly below average.

The winter towards **2008** obviously brought no clear worsening of the prey offer. The number of broods again increased, even if not clearly. Indeed the number of eggs then already was clearly lower. The losses then were rather inconspicuous. (late egg laying)

2009 then again was a year with very late egg laying, very low numbers as well for the broods as for the eggs. The losses during the broods were normal. (snow periods with dead recoveries)

On this basis the year 2010 then brought a very early egg laying, the again lowest number of pairs, but of broods: Several ♀ and also (less) ♂ bread twice. All success numbers were as high as ever before. In addition the losses again reached the until then lowest values. (The micro-rodent population obviously had increased clearly since 2009. Indeed the prey was scarcely available beneath the snow cover. The micro-rodent population was high during the breeding period, thus the high success values and the low losses.)

3.3 Broods

For this study 520 broods were analyzed, 106 (20.4%) of these remained unsuccessful. About 35 were only found, when they already had been abandoned. Except for six (not accessible or found to late) the young of all successful broods found could be ringed. The pulli not ringed (guessed: n=25) comprised about 1% of all young of the total study interval. So we guess that the breeders controlled unbanded, up to 99% were immigrants.

Laying date

Laying date already above has been analysed to characterize the years. Here we will depict, how it looks summarized over all years of the study. In figure 33 a very strong increase of the values from the beginning of March up to a maximum in the first decade of April, and subsequently a fairly regular, less steep decline are visible.

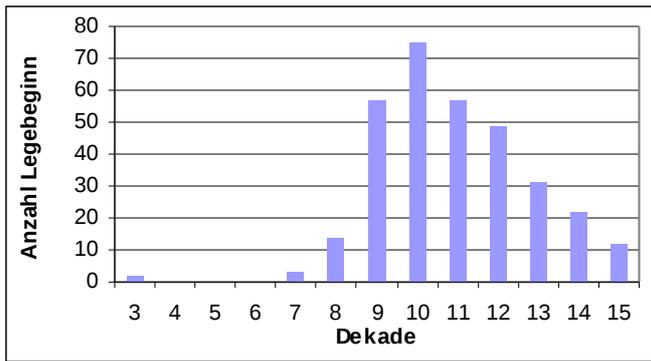


Figure 33: Summed egg laying for the broods with sufficiently known data in the first half of the year; n=323; The tenth decade corresponds to the first decade of April

Clutch size

Figure 34 shows that in first clutches 6-7 (8) eggs are normal. Clutches of five eggs are clearly rarer. For the majority of clutches with a lower egg number, following the circumstances there was the suspicion that here after a disturbance the ♀ had layed the residual eggs, already in development in the ovary, at a new site. There can be no certainty, as a control of the parent birds of an abandoned brood naturally is not possible.

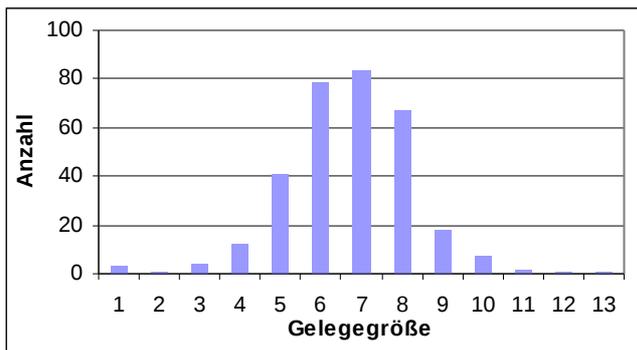


Figure 34: Clutch size of first clutches; n=320

Clutch size does not remain identical over the total breeding interval. With increasing scattering it steadily decreases from broods with egg laying during April to those during June (fig. 35).

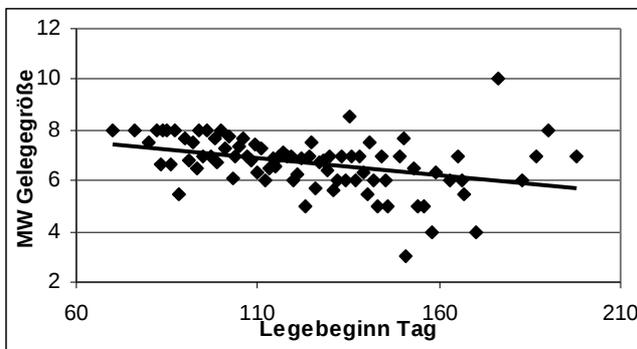


Figure 35: Dependence of clutch size on egg laying: only first broods for both parents; days since onset of the year; n=311

Fledging success in relation to clutch size as well decreases fairly regularly and clearly with egg laying (fig. 36).



Figure 36: Decrease of the breeding success with egg laying: part of young fledged in % of clutch size; only first broods for both partners; n=311

Multiple broods

This subject and also the circumstances of a mate change for a second brood have been communicated in separate papers (KNIPRATH & STIER 2008, KNIPRATH & STIER-KNIPRATH 2011), so that the description here may be missed. There have been no new aspects since.

3.4 Breeders

All statements exclusively are based on ringed owls. Among 537 broods for 424 (79.0%) the σ and for 462 (86.0%) the ♀ could be controlled. As several of these owls breed manifold (σ up to eight and ♀ to nine fold), in reality 236 σ and 283 ♀ had shared in these broods. 71 of the σ (30.1%) and 75 of the ♀ (26.5%) had been ringed as nestlings and thus were known by their exact age. The mean age of the brood males of known age summed over all their broods was 1.75 years (with a range of 1 to 6 years), that of the ♀ 1.53 Years (1 to 7 years). The differing mean age of σ and ♀ already has been noticed in the chapters "Rank of the villages" (fig. 10) and "Age of the breeders by years" (fig. 27), as well as the heavy oscillation of the mean age of the breeders over the years. In figure 37 now it becomes clear that for both sexes there seems to be a correlation between the population density and the mean ages of the breeders over the years, which indeed is counter rotating.

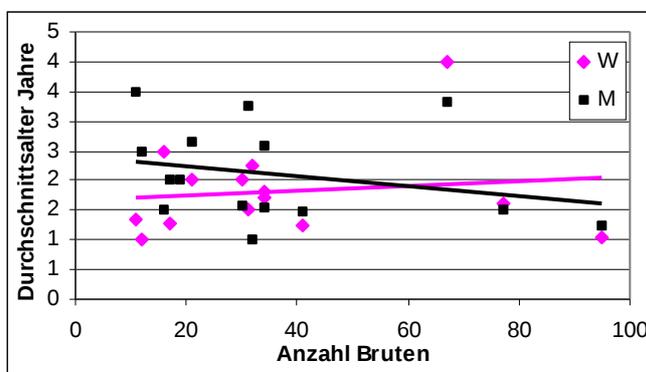


Figure 37: Correlation between population density and mean age of the breeders of exactly known age (σ : n = 123; ♀ : n = 75)

As there is a much greater number of breeders, which had immigrated with unknown age, their data were checked for usability in this context: All immigrants at their first brood have been classified as yearlings. The average age of all over all their broods for the ♂ has been 1.95 years (165 individuals with 299 broods) and for the ♀ 1.51 years (237 individuals with 385 broods). The mean age of the immigrated ♀ as compared to that of the ♀ of known age (1.53 years) may indicate that the classification of these as yearlings is right. The difference in the ♂ for the 1.75 years (of the ♂ of known age) and of the 1.95 years (of those immigrated with unknown age) is not significant ($P > 0.5$). Until further information immigrants of both sexes may be classified as yearlings.

Figure 38 on one hand clearly shows the difference in the average age between the ♂ and the ♀ and in addition that in both sexes there is an – even not to great – correlation between population density and the mean age of the breeders: In years with more broods it is slightly lower. The causal relationship of course is inverse: By the fact that in some years more yearlings (also immigrated ones) are integrated into the population, the average age of the latte one lowers.

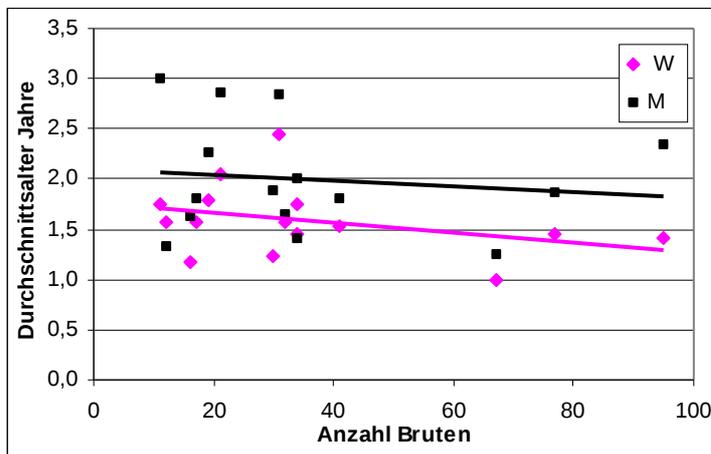


Figure 38: Correlation between the population density and the mean age of the breeders originally immigrated (♂: n = 165; ♀: n = 237)

Even if it seems certain that the immigrants mostly are yearlings, these two groups of breeders (birds with known age and immigrants of unknown age) at least for the next analysis will be preserved. We will occupy with the question, how great the part of the age-groups is in the broods. The comparison in figure 38 demonstrates that obviously there is no noteworthy difference between the groups. In consequence the discrimination as breeders with known age and as immigrants is given up. A further simplification consists in summing up the breeders into three age-groups: yearlings (about one year old), medium aged ones (2-3 years old), and old ones (>3 years). This simplified age structure in the breeding population in the study area thus looks as given in figure 40. It appears that in the ♀ the part of yearlings is clearly higher and correspondingly that of the further age-groups generally lower.

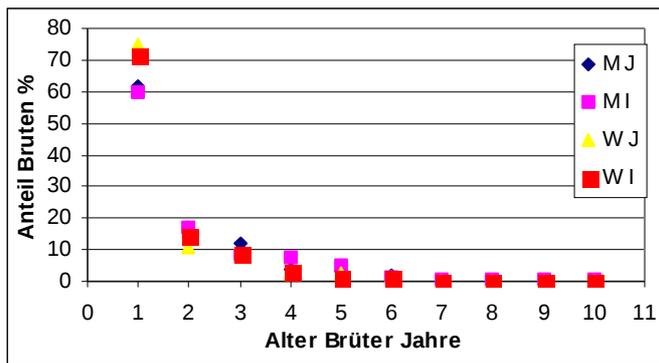


Figure 39: Part (%) of the age-groups of the owls in the broods (MJ = yearling ♂, MI = immigrant ♂, WJ = yearling ♀, WI = immigrant ♀ of the figs. 37 and 38)

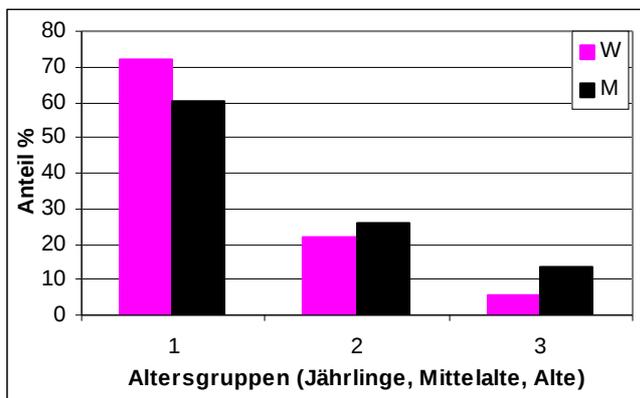


Figure 40: Age-structure of the breeding population by sex and age-group (yearlings (ca. 1 year old), medium aged ones (2-3 years), and old ones (>3 years old))

3.4.1 Origin of breeders

The breeding population *of the single years* is composed of three fractions: the own recruits (for each year only the new ones), the breeders of the past years as having stayed (in part site-faithful, in part having moved), and the immigrants (for each year only the new ones). The number-relation of these may be taken from table 3. Here we did not count: recruits, which only two years after ringing had been controlled (they should have bred already somewhere the preceding year without control). It becomes visible that the annually new immigrants (i.e. earlier immigrants, which already had bred in the study area, not included) alone make up >50% of the breeders. In that this part in the ♀ was still clearly higher. The ♂ more often stayed (ore survived), as well as recruits as also as breeders.

	part ♂	part ♀	both tog.
recruits	16,96	11,39	14,08
immigrants	45,24	63,33	54,60
stayed	37,80	25,28	31,32

Table 3: The breeders in % as belonging to the groups of origin (n=696)

The part of the recruits, i.e., that of the yearlings, narrowly ($R^2=0.79$) is related to the number of broods of the respective year (fig. 41). The attempt to find a direct influence of the preceding year failed (fig. 42). Indeed in this figure it is interesting that in years with medium numbers of breeding pairs (about 35), the highest parts of

yearlings were found. So the part of yearlings in the breeders of a year far-going is correlated with the number of broods at all, what certainly means that both are depending on the prey situation of the preceding winter and of the spring time.

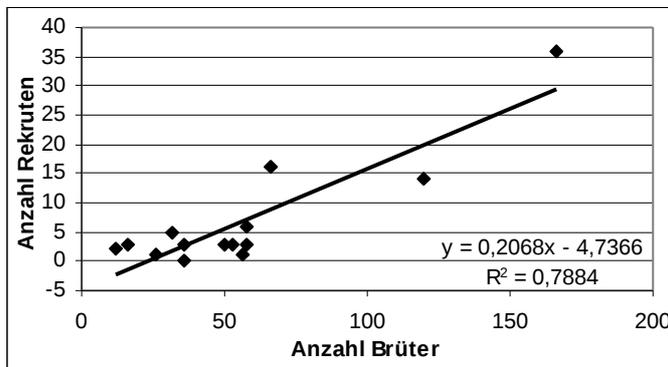


Figure 41: Correlation between the total of breeders and the number of recruits of the years (n=98)

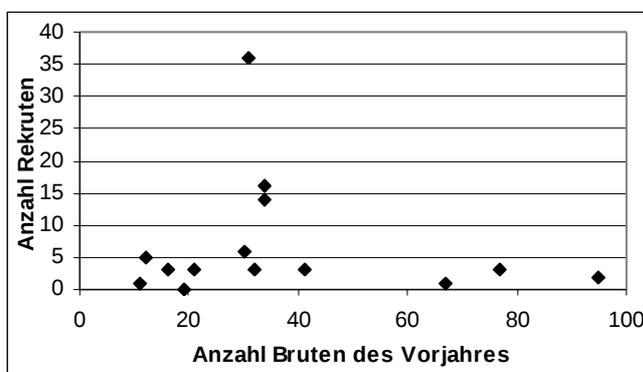


Figure 42: Number of recruits of a year and number of broods of the preceding year (n=98)

Also the number of immigrants tightly ($R^2=0.85$) was connected with the total number of broods of the actual year, but not with that of the preceding year (no fig.). The least tightly ($R^2=0.5$) was this correlation for the staying breeders.

The distance of origin as well for the birds ringed as nestlings as for those ringed as breeders was twice as great for the ♀ as for the ♂ (table 4). No young bird has been recovered in the nest-box of his birth. Among the ♂ owls ringed as adults 61, for the ♀ 38 have been faithful to their preceding breeding site. Among these there were 35 faithful pairs. (For partner-fidelity and the contrary of it, divorce, see KNIPRATH 2011.)

All preceding analyses on the origin had as basis the breeders of the single years. If we look at the origin of the total of the owls controlled as breeders (i.e. each owl counted only once), for the ♂ a part of 28.57%, for the ♀ of 15.25% is found with birth in the study area. Here we find a greater fidelity of the ♂ to their birth-place and with that also their lesser inclination to farer wandering.

On the other hand these number as well signify that less than one third of the breeders of the study area had hatched there.

	juv	ad
♂ (n)	64	127
♂ median km	5,51	0,1
♀ (n)	55	105
♀ median km	9,2	0,2

Table 4: The median of the distance of origin of the breeders of the (yearly) first broods

3.4.2 Abode of breeders

As well as the origin of the breeders also their abode after a brood may give interesting information. First we here mention the 35 faithful pairs, of which 34 had stayed at their breeding place and only one had moved to the neighbouring village. Among the 327 breeding ♂ controlled 187 (51.2%), among the 354 ♀ 210 (59.3%) in later years no more have been controlled again. As the years 2009, 2010, and even more 2011 only had a very low population of breeding pairs, it was (different from an earlier study: KNIPRATH 2007: 5) not necessary to exclude these last years of the study interval. The breeders controlled again either were found at their former breeding site or had moved. Besides the site-fidelity in table 5 we also indicate, whether mate-loss had happened. We here do not include the behaviour of the faithful pairs. All together it becomes apparent that among the ♀ a clearly greater part was not faithful to the breeding place than among the ♂. Obviously the loss of the mate for the ♀ is an important, for the ♂ a less important reason to change the breeding site.

	♂		♀	
	N = 138		N = 142	
	stayed	moved	stayed	moved
uncertain	35 (25,36%)	49 (35,51%)	25 (17,61%)	86 (60,56%)
mate-loss	27 (19,57%)	27 (19,57%)	6 (4,23%)	25 (17,61%)
summ	62 (44,93%)	76 (55,07%)	31 (21,83%)	111 (78,17%)

Table 5: Abode of the breeders (without faithful pairs); "uncertain" means: At one of the broods compared, the mate was not controlled.

Then we followed the supposition, the decision for or against staying at the breeding site could have been influenced by the success of the last brood. The majority of the unsuccessful breeders (♂: 25 = 59%; ♀: 42 = 67%) was recorded again breeding not at all. (For the breeders with success the numbers are: ♂: 57%, ♀: 59%.) Among the unsuccessful ones altogether only 38 have been recorded again. For a further analysis this seems to be to less.

3.4.3 Laying date and age

In chapter 3.2.4 we already analysed the year to year variation of egg-laying. The decision for an earlier or a later egg-laying also could depend on the age of the owls. Figure 43 shows that egg-laying in both sexes on average increases with increasing age.

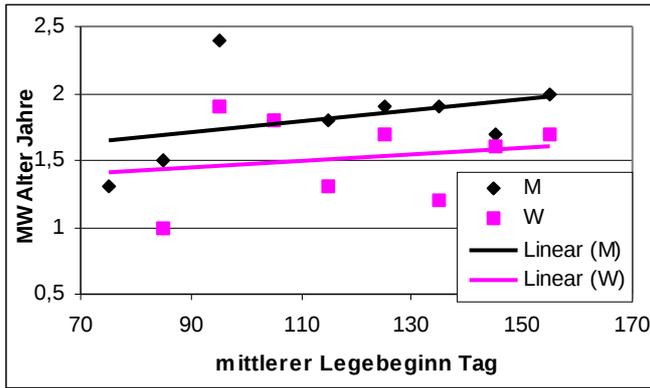


Figure 43: Correlation between age of the breeders and mean of egg-laying (in days after January 1rst) (n= 321 ♂: 263 ♀)

3.4.4 Breeding success and age

We should test, whether life-experience and/or breeding-experience do have an influence on the breeding result. For this, immigrants – as substantiated above – at their first brood were counted as yearlings and the data from outside the narrower study area and interval were included. Table 6 shows that the yearlings generally had the better success values, whether the unsuccessful broods were included or not. The differences are not significant (all $P > 0.1$). In all years of the study yearlings participated in the broods. So it is unlikely that the effect is based on years with a higher part of yearlings.

	♂		♀	
	n	mean	n	mean
all yearlings	285	5,07	389	4,71
all older	194	4,88	147	4,41
yearl. succ.	311	5,49	337	5,40
older succ.	112	5,40	124	5,20

Table 6: Breeding success (mean number fledglings) of yearlings and of older birds

Then we tested with all data available (i.e. also from the pre-study and the surroundings), whether there was any difference in the breeding success within the group of older owls. Figure 44 of course shows well fitting polynomic regression curves, but – besides a decrease of the values in both sexes from the yearling to the two years old birds with a following, slight bettering – without otherwise any interpretable course.

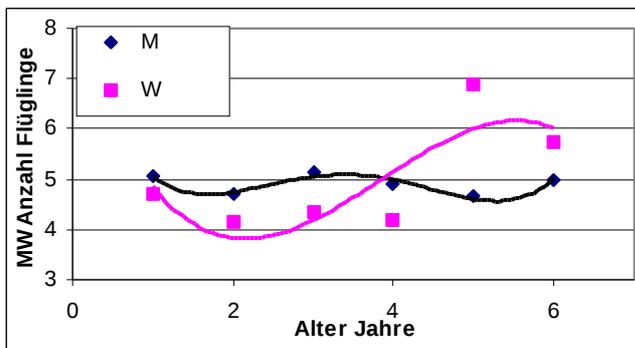


Figure 44: Dependence of the mean number of fledglings from the age of the breeders (σ : $R^2=0.68$; φ : $R^2=1.015$)

Nevertheless it seemed possible that as well the two sexes as also the age of the breeders (by age groups) had a different influence on the success-values (eggs, hatchlings, and fledglings). Figure 45 indeed shows a diminishing success in both sexes until medium ages in egg-numbers, in the σ even up to the higher age, this latte indeed not in the φ . In contrast, the older φ are clearly better than the younger age groups. When looking at the results concerning hatchlings, the relation between the three age groups remains constant and also the progression of the old φ towards the medium aged ones (fig. 46). Concerning the result of the elevation phase we detect an increase in the number of fledged young in contrast to the medium aged birds (fig. 47). It is interesting that the yearlings (σ) slightly can preserve their prominence from the egg number up to the number of hatchlings. Inversely the old φ kept their one until fledging of the young.

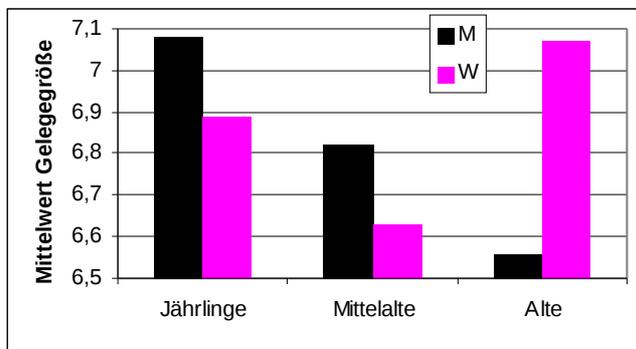


Figure 45: Influence of the age of the breeders (for the definition of the age groups see fig. 40) on the mean clutch size (n = 1.015; σ : 479, φ : 536)

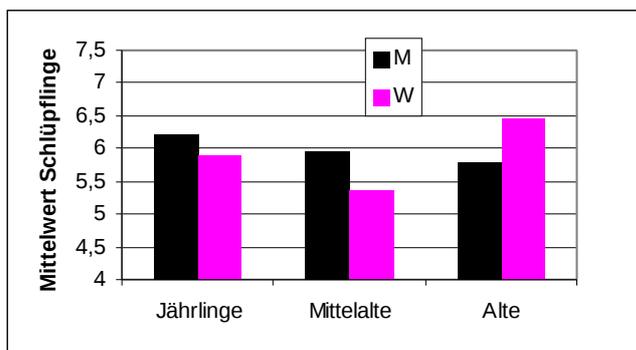


Figure 46: Influence of the age of the breeders on the mean number of hatchlings (n = 1.015; σ : 479, φ : 536)

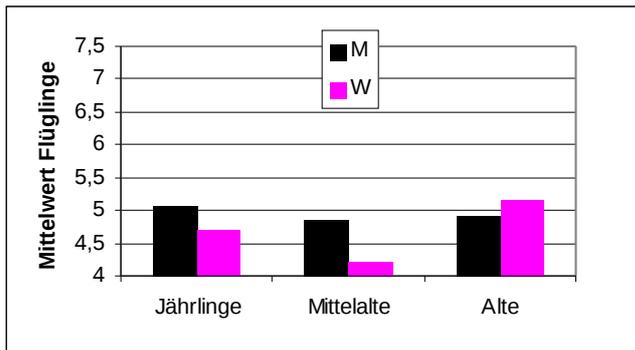


Figure 47: Influence of the age of the breeders on the mean number of fledglings (n = 1.015; ♂: 479, ♀: 536)

The absolute result of the incubation and the brooding phases indeed don't give the right impression. The work of the sexes and the age groups during phase 2 (incubation) only shows clearly, if we compare, how many pulli hatched relatively to the egg number (fig. 48). Here at first is striking that the old owls (>3 years) are more successful than the two other groups. The medium aged ones in both sexes – in the ♀ much more prominent than in the ♂ - are the poorer age group. Figure 49 then demonstrates that the ♂ with on growing age improve in elevating the hatched young. In the ♀ also in this phase the medium aged ones are the poorest ones. In the balance (fig. 50) it becomes apparent that in total the older ones are better than the yearlings and clearly better than the medium aged ones. This effect in the ♀ is much clearer than in the ♂.

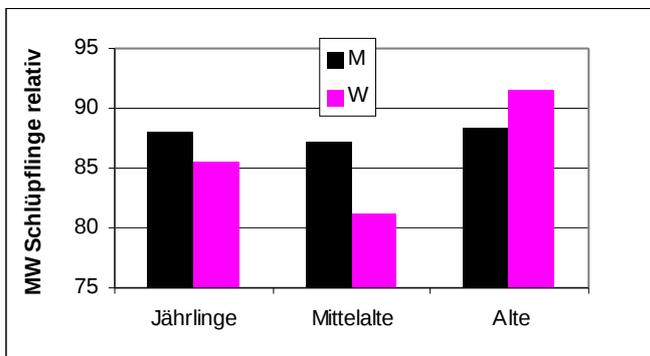


Figure 48: Influence of the age of the breeders on the mean number of hatchlings from 100 eggs

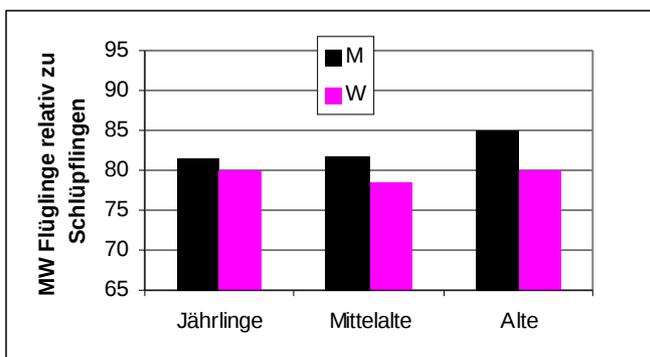


Figure 49: Influence of the age of the breeders on the mean number of fledglings from 100 hatchlings

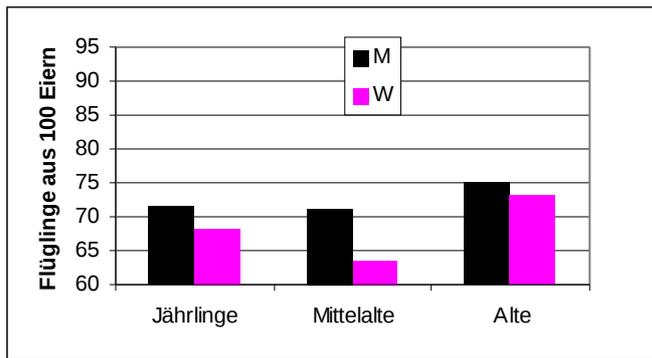


Figure 50: Influence of the age of the breeders on the mean number of fledglings from 100 eggs

As a simple examination, whether somewhere any error would have happened when transferring numbers, for both sex means were calculated over all their broods. It resulted that they were not identical, what they logically should have been: The differences for all three success values (figs. 45-50) were at 0.2-0.5. The supposition that the reason for these differences would to be looked for therein that for both sex all values available had been taken as basis and not only those broods, for which ♂ and ♀ were known, was confirmed, when the calculations for the figures 45-50 now for the new figures 51-54 were done only pairs with known mates.

The figure 51 (clutch size) compared to figure 45 demonstrates no important difference: As yearlings the ♂ are the best ones and loose considerably towards age. The ♀ as well are the best ones as yearlings, then loose and towards higher life age again win in efficiency.

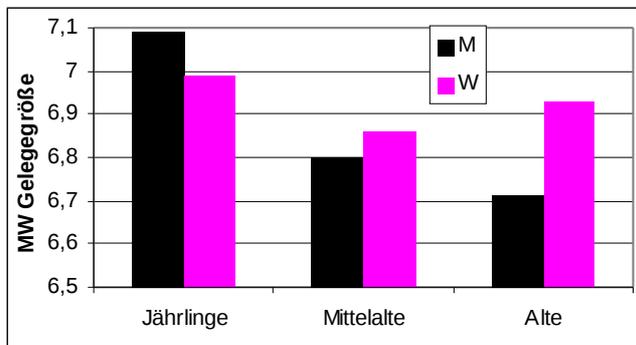


Figure 51: Influence of the age of known pairs on the mean clutch size (n: ♂ and ♀ = 462)

As has been shown above that the meaning of means of hatching and fledging success is low, the numbers here no more are analyzed. Figure 52 directly gives an impression of the performance off the breeders during the incubation phase: The values are closer together than in figure 48 and the influence of the age in the ♂ is low. Solely in the ♀ again the older ones are more successful. Not different is the influence of the age of the pair-mates during the phase of brooding and the further elevation of the young until fledging (Fig. 53). Compared to figure 49 the values here are slightly closer together. The relations between the age groups indeed remain preserved. In the total balance the owls of higher age of both sexes (fig. 54) are

better. Merely in the ♀ the medium aged ones are still less successful than the yearlings. Compared to figure 50 again the values are closer together and the relations remain preserved.

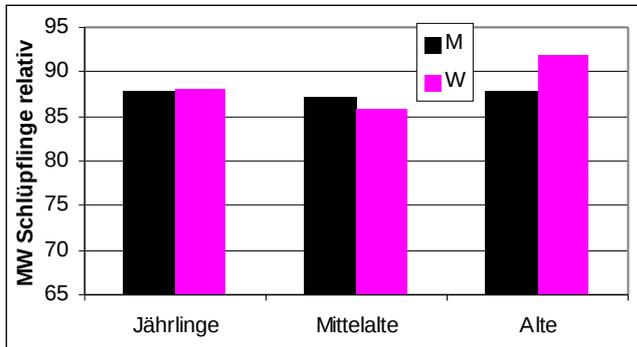


Figure 52: Influence of the age of the mates of known pairs on the mean hatching success of 100 eggs

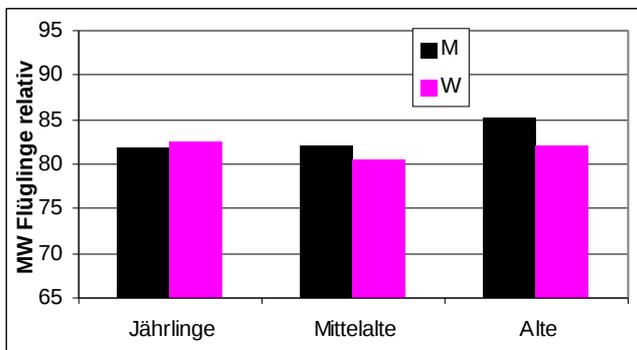


Figure 52: Influence of the age of the mates of known pairs on the mean fledging success of 100 hatchlings

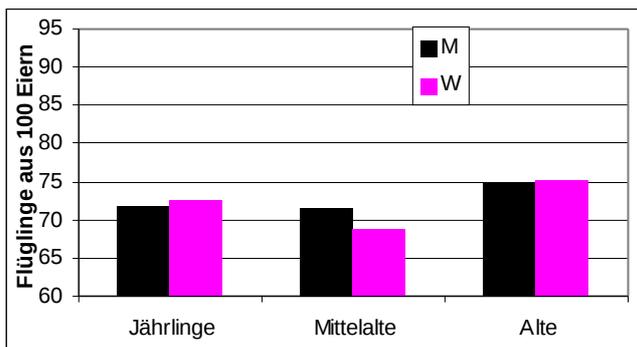


Figure 54: Influence of the age of the mates of known pairs on the mean fledging success of 100 eggs

The difference between the two sexes concerning the age-depending capacity again will be stressed in chapter 3.4.6 under the aspect of mate-combinations.

3.4.5 Breeding success and laying date

The average egg-laying of the years was positively correlated with the breeding pair density (chapter 3.4.3) and oscillated like these from year to year. It should be controlled, whether the breeding success was depending on the laying date. Figure

55 demonstrates that years with early egg laying were those with higher egg-numbers. Also all years added, clutch size was greater with earlier egg laying, but not as clearly (fig. 56). So this only in part was an effect of the years. In addition it is visible that this influence in the course of the breeding season obviously again turned back, and that this correlation is not linear. The polynomial regression clearly better represents the connection ($R^2=0.28$) than the linear one ($R^2=0.08$). This is the same for the breeding success (fig. 57). In chapter 3.4.3 we had demonstrated that it are preferably the older breeders to begin earlier with breeding.

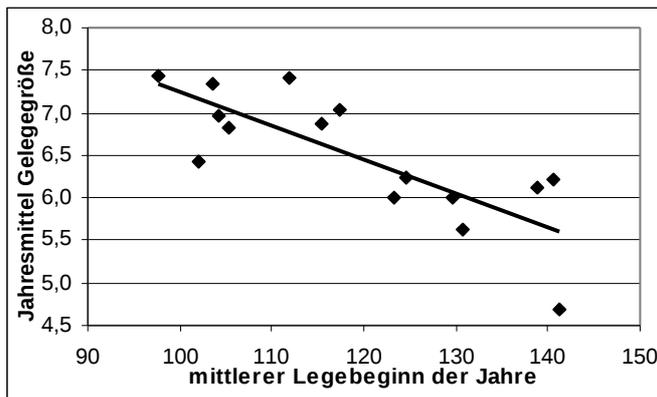


Figure 55: Correlation between clutch size and egg-laying, yearly mean each (only first broods; n=408)

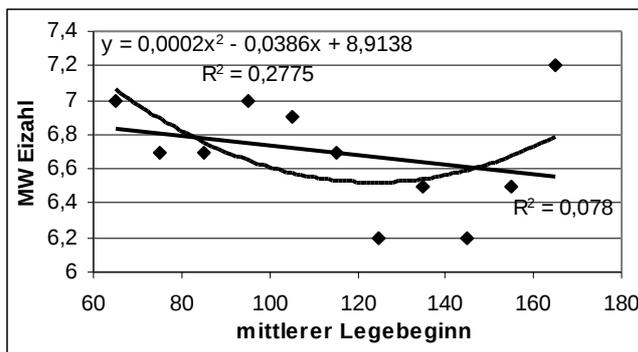


Figure 56: Correlation between clutch size and egg-laying over all years (only first broods; n=408)

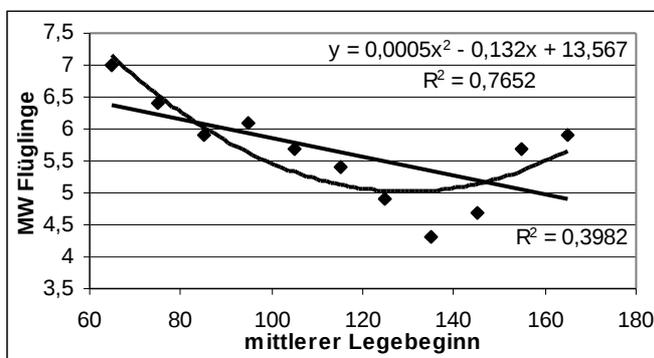


Figure 57: Correlation between mean breeding success (fledglings) and mean egg laying over all years (only successful first broods)

3.4.6 Pairs

As Barn Owls during breeding have a strict duty sharing, the success always is depending on both mates. So the pairs were judged as unities and studied as such. Among the 347 pairs, for which both mates are known, 72 had been faithful from the preceding brood, 19 had separated (divorced), and 256 were newly formed ones (here all broods, i.e. second broods considered). The circumstances of the divorces already been analysed (KNIPRATH 2011).

Among the 35 pairs, which had been faithful from brood A to brood B, 25 stayed in the original box, none more in the village. The only one, which has moved to the neighbouring village, had stepped aside construction works. So, faithful pairs stay at their breeding site or in its nearest neighbourhood.

Pair formation

Each young owl and as well widowed or divorced older owl needs a mate for the first or next brood. The two sexes may use different strategies to find a new partner (EPPLE 1985). The ♂ preferably are site-faithful and display, the ♀ rather vigil and seek. Meanwhile it has been proven that mating is preceded by an examination of possible partners (KNIPRATH & STIER-KNIPRATH 2011). It seems self-evident that the sense of a mate choice is to find one of possibly highest quality. Where of this quality in fact consists, can't easily be found. Measurable resp. countable in each case is the result of the breeding attempts, which indeed serves to render the genes.

If the owls in fact chose for quality, this firstly should be measurable at a mate-change. As a measure of the quality of the preceding as of the new mate in many cases the life-production in fledglings was at our disposal. Simultaneously it could be checked, whether the owls, when looking for a new mate, did make use of different strategies, i.e., whether they stayed or moved after the loss of their mate. Second and replacement broods here are excluded, as at that time only a very restricted number of possible mates are at disposal. The relating behaviour has been studied in an earlier paper (KNIPRATH & STIER 2008)

The numbers belonging to this comparison are composed in table 7. The numbers of individuals compared differ from those in table 5 as not for all sufficient data on life production of the partners have been at disposal. It was obvious that ♀ az new pairings found a mate of lesser quality, if they stayed, all other owls indeed found one of better quality. Only the profit of the ♀, which had moved, was significant (EXCEL: P > 0.5).

	♂		♀	
	n	difference life-production fledglings	n	difference life-production fledglings
stayed	32	1,6	10	-1,4
moved	43	2,3	29	6,3
summ/mean	75	2	39	5,1

Table 7: Mean difference in mate quality (life-production fledglings) between former and new partner at new-pairing, discriminated for stayed and moved breeders

Then we could analyze whether at the mate choice a selection by age happened. As a part of the population was ringed, the owls were known by their age (see chapt.

3.4). There to all yearlings as well as the immigrants were taken as being one year old, even if many of them at their first brood not had been 12 months old and certainly there was the one or other immigrant, who was older than one year.

Table 8 on one hand shows the part of the age-groups in the total breeder population over the years and then the part of the combinations at random pairing (strongly framed). Here we included as well the breeders with exactly known age as the immigrants (n=777). Basing on 312 pairs for which the age was known, table 9 comprises the real parts of the age combinations. The comparison between the tables 8 and 9 shows that the part of pairs with mates of a similar age (grey fields) in reality was clearly higher than could be expected basing on the part of the age groups in the total breeder population.

	part orig.	yearling ♀	medium ♀	old ♀
part orig.		73,30	20,75	5,97
yearling ♂	60,00	43,98	12,45	3,58
medium ♂	26,35	19,31	5,47	1,57
old ♂	13,65	10,01	2,83	0,81

Table 8: Expected part of the age-group-combinations: yearlings (1 year old), medium aged (2-3 years), old ones (>3 years old) at the age-combinations in the population by hazard (all breeders; n=777)

	n orig.	yearling ♀	medium ♀	old ♀
n orig.		233	58	21
yearling ♂	187	53,85	4,17	1,92
medium ♂	84	14,74	10,58	1,60
old ♂	41	6,09	3,85	3,21

Table 9: Real part of age group combinations in % (n=624)

In 33 faithful pairs (only from the first brood in a year to that in the following year) 18 (54.55%) belonged to the same age group. These are more than they would be by hazard (table 8: 43.98+5.47+0.81=50.26) and clearly less than they were in reality (Tab. 9: 53.85+10.58+3.21=67.64).

How newly married owls really have chosen with respect to age is shown in table 10. To use the same time-scale for the comparison between old and new mate, the average age calculated for the old mates was heightened with 1. So the change from the anterior to the new mate fictitiously took place at the beginning of the new breeding season, even if then already some of the old partners didn't exist anymore.

	yearlings		medium old (2-3 Jahre)			old (>3 Jahre)		
	n	partner	n	anterior partner	new partner	n	anterior partner	new partner
♂	204	1,23	58	2,35	1,38	30	3,07	1,93
♀	236	1,58	36	2,94	2,22	6	4,00	3,33

Table 10: Mean age of the anterior and the new partners after change

As a further selection-criterion at mate choice, ROULIN et al. (2001) have proposed the plumage colouration. The five types of the under part coloration as used here have been described in their frequency during the first ten years of the study

(KNIPRATH & STIER-KNIPRATH 2006). Table 11 gives the relative part of these types in the total population and the parts in the combinations at hazard (strong frames) as calculated there from. Table 12 indeed gives the real part of the combinations in % (strong frame). Even if there were smaller differences, we did not succeed in seeing therein a system of preference. So we can accept that the Barn Owls of the study area do not choose by the under part coloration.

		♂ type 1	♂ type 2	♂ type 3	♂ type 4	♂ type 5
	Part/popul.	2,62	20,94	17,8	24,08	34,55
♀ type 1	1,28	0,03	0,27	0,23	0,31	0,44
♀ type 2	8,12	0,21	1,70	1,45	1,96	2,81
♀ type 3	9,40	0,25	1,97	1,67	2,26	3,25
♀ type 4	14,53	0,38	3,04	2,59	3,50	5,02
♀ type 5	66,67	1,75	13,96	11,87	16,05	23,03

Table 11: Relative part in % of the five types of under part coloration in the total population and the calculated parts in the combinations in pairs at hazard (strong frame). The combinations of same colour types are shaded.

		♂ type 1	♂ type 2	♂ type 3	♂ type 4	♂ type 5
	n in pairs	5	59	57	81	76
♀ type 1	5	0,00	0,36	1,44	0,00	0,00
♀ type 2	29	0,00	1,08	3,24	5,76	0,36
♀ type 3	29	0,00	2,52	1,80	3,96	2,16
♀ type 4	45	0,00	4,32	4,32	4,68	2,88
♀ type 5	170	1,80	12,95	9,71	14,75	21,94

Table 12: Real part in % of the five types of under part coloration in the total population and the calculated parts in the combinations in pairs at hazard (strong frame). The combinations of same colour types are shaded.

Success of pairs

In chapter 3.4.4 the success of breeders had been studied by age of life for both sexes separately. But indeed not individuals of different age do breed but pairs. So there could be an effect of the combination. Here we compare the three age groups as already introduced above: yearlings (about 1 year old), medium aged ones (2-3 years), and old ones (>3 years) in the total material.

Taking clutch size (fig. 58), the yearling ♂ are most successful together with an old ♀, the medium aged ones with an old ♀, old ones reversely with a medium aged ♀. For the success of breeding the age of the ♀ has no influence for the yearling ♂ (fig. 59), only little for the medium aged ♂, but indeed for the old ♂: They are most successful with a yearling ♀ and least of all successful with a medium aged ♀. During the time of rearing the young the picture only slightly alters (fig. 60). Here it is conspicuous, how little successful medium aged ♂ are together with yearling ♀. The total balance (fig. 61) shows that the choice for the yearling ♂ is not critical; together with a medium aged ♀ they are most successful. For medium aged ♂ a yearling ♀ is the worst choice and for old ♂ that of a yearling ♀ the most successful strategy, the of an similarly old ♀ the not essentially worse one. Reversely for a yearling ♀ the choice of an old ♂ is the best one, even if the least probable one. The most recommendable

choice for her is the choice of a ♂ of an about similarly aged ♂, as it really is visible in table 9.

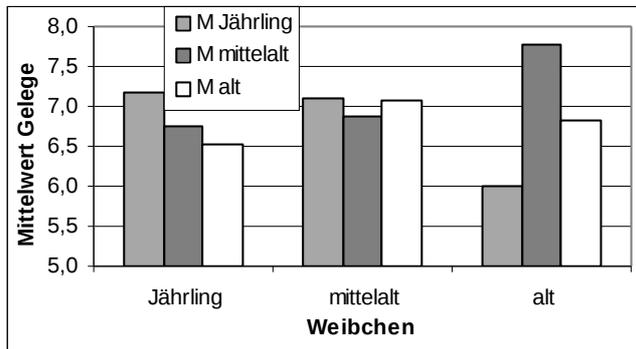


Figure 58: Mean clutch size of the nine possible age combinations by sex (n=422)

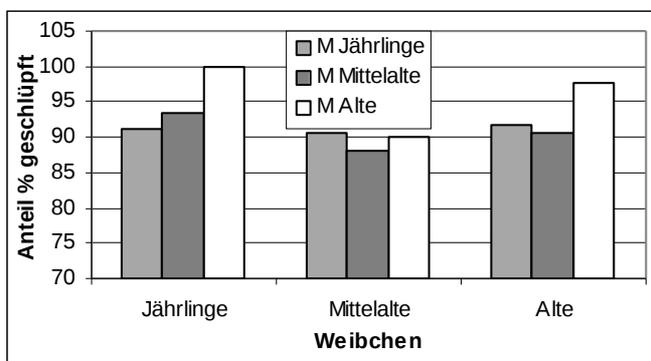


Figure 59: Hatching success in % of the nine possible age combinations by sex (n=422)

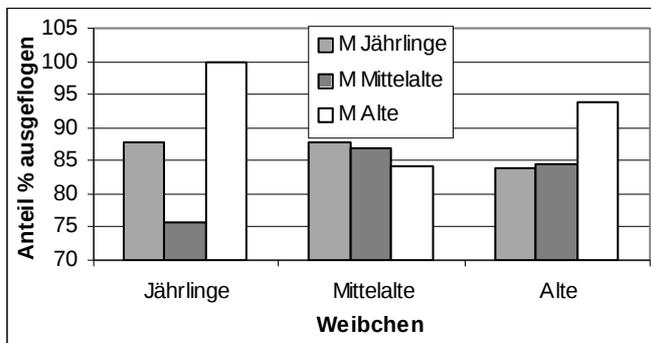


Figure 60: Fledging success in % of the nine possible age combinations by sex (n=422)

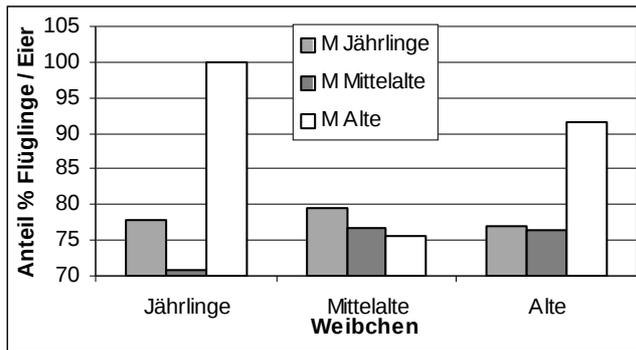


Figure 61: Total balance

Breeding success and faithfulness

This part already has been published (KNIPRATH 2011: 79)

4 Discussion

4.1 Breeding localities and sites

As in the posting of the boxes there was no preference of certain villages or regions throughout the study area, the preference of a few part-regions by the owls not can be attributed to differences in the offer of boxes. The unequal distribution of the broods (fig. 5) is the result of a choice by the owls. It is unknown by which criteria the owls selected the villages and inside these the boxes. The frequency of use of the single boxes also has to be judged in front of the background that even in peak years there always was a great surplus in boxes, even if Kestrels occupied a greater number (up to 30%) of these. Also then the owls had the choice. In a single year in one village (Odagsen) all five (!) of the boxes hanging there had been occupied by pairs, there was no bigyny. That also in another study (KNIPRATH 2007) a choice by the owls could have been demonstrated astonishes afterwards, as there in almost no village more than one box was present. It is astonishing as well that we did not succeed in demonstrating that the preferred sites were those with more eggs and more young (figs. 11-13).

JAHNEL (1989) contradicts the interpretation here that the special height of church towers rather doesn't play a role. In his study area, the Hess Main-Kinzig-Kreis, 70.5% of the broods took place in boxes in church towers, although their part amounted only 45.98%.

The further reflections in connection with the breeding site selection in KNIPRATH (2007: 35) here not are repeated, as there are scarcely new aspects. Concerning the choice success it is astonishing here that the own yearlings, as far as they were ♂, had as little success as the immigrated ♂ of unknown age. We are inclined to make the note: "But they indeed new the quality of the boxes, in each case better than the immigrated owls." This rally is true. On the other hand they were known to the old-established ♂ as "children" and perhaps therefore they had fewer chances to be successful. In addition the majority of yearlings bread in the better years. In these indeed due to the altogether higher numbers of broods there were more adult ♂. The occupation of one of the preferred boxes then again is more difficult. For the ♀ the success has to be judged differently. The less choose a breeding site than the belonging ♂ (EPPL 1985).

When newly settling and also when changing the breeding locality the owls most obviously make their choice. They really had a chance as even in the years with highest brood numbers and under taking in account that Kestrels used boxes as well, still 30% of the boxes remains unused. To a choice quality criteria are belonging, by which a decision is made. The design of the boxes cannot be one, as these are mostly identical and also posed following similar criteria. The more probable the altitude of the village plays a role (figs. 6-9). Whether it is the general prey availability, seems to be questionable as the directly depending success numbers don't give clear indications (figs. 11-13). The more a bad prey availability in the years of very low populations of smaller mammals could be of signification.

4.2 Yearly oscillations of the success values

All authors (last JAHNEL 1989, GRAEF 2004, KNIPRATH 2007, HERRMANN et al. 2010) agree that the brood numbers in part heavily oscillate from year to year. Those oscillations as well concern clutch size (GRAEF 2004, KNIPRATH 2007), the losses during incubation and brooding Huderzeit (GRAEF 2004, KNIPRATH 2007), and also egg laying (KNIPRATH 2007, KNIPRATH & STIER 2008). For the region around Dessau HERRMANN et al. (2010: fig. 2) have shown that the numbers of broods and the success values (young ringed) during the years 2000 – 2010 impressingly parallel. Here indeed we depict that the oscillations of these values very clearly were asynchronous (figs. 20-22, 24, 25, 29). The biologic reasons for that not only resulted from the year to year oscillations in the prey availability but also of that within the years. The total number of broods depended on the breeding success in the preceding year, together with the prey availability over winter. This availability during the months of February – April influenced egg laying as well as clutch size and that in the months of Mai – July the elevating success. The uniformity of the course around Dessau (HERRMAN et al. 2010) makes derive that there also the development of the rodent population was very constant.

Concerning egg laying from the data from the study areas county Celle, Barnbruch, county Potsdam-Mittelmark, and county Northeim (KNIPRATH 2007: fig. 46, KNIPRATH et al. 2008) an advancement has been deduced. The data from the northern part of the county Northeim now include five more years (fig. 29). From that figure an advancement no more can be deduced. Whether this also is true for more areas still has to be studied. As the presumed cause, the global warming, is ongoing, a change of this trend hardly is imaginable. The only clear thing is that for strong oscillations of the values already very few extreme values may lead to an entire change of the trend as established statistically. The causes for these strong oscillations could be, following the communication of a meteorologist in the TV, the always more frequent occurrence of extremely cold and long winters in Europe, despite all global warming. After those winters, which very strongly limit the prey availability for the owls, these latter ones later begin breeding (MEBS & SCHERZINGER 2000: 78).

4.3 The breeders

The part of the adult bird controlled annually amounts to >80% and thus mostly is at a similar level as that of TAYLOR (1994) and R. ALTMÜLLER (KNIPRATH 2007). Any comparison with these studies so not has to be limited.

Origin (structure of the population)

Among the 696 breeders here, which had been controlled, for the ♂ apart of 28.57%, for the ♀ of 15.25% had fledged in the study area (ca. 520 km²). In the population around Lachendorf studied by ALTMÜLLER (KNIPRATH 2007) comprising 220 km² this part for the ♂ is at 36.2, for the ♀ at 22.4% (values calculated from the original data). Thus both parts are clearly greater than in the population studied here. If we totally logically deduce that at otherwise similar conditions the part of the “own descendants” increases with increasing extent of the study area, this relation truly should be inverse. Thus the conditions are not equal. So we suppose that our population is depending on more immigration from outside. DE BRUIJN (1994) for his two Netherland populations had concluded from the calculated wins and losses for young and old owls that one of them has produced a surplus and the other one indeed was depending on immigration from abroad. Whether we, for a species, whose young regularly to a great extent disperse, may conclude from a slightly smaller part of own recruits that immigration is necessary, remains uncertain. In contrast it seems certain that for both populations emigration of young owls is not caused by an eventual need of the original population for its maintenance.

The greater inclination to wander and with it also the greater distance of origin of the ♀ as ascertained here, as well at the new settling of recruits as at the moving of owls ringed as adults, corresponds to the numbers of R. ALTMÜLLER (KNIPRATH 2007: 23, 25).

Also at the breeding site fidelity there is correspondence between the studies. The ♂ stayed sooner than the ♀ and travelled when moving, less far. The loss of the brood mate was a reason for dismigration sooner for the ♀ than for the ♂ (TAYLOR 1994: 198; KNIPRATH 2007: 26).

Age

The age structure as discovered here (fig. 40) with for example more ♀ yearlings than ♂ ones mostly corresponds to that found for the population around Lachendorf (KNIPRATH 2007: 22).

The classification of immigrants as yearlings also therefore is justified as after KNIPRATH (2013) and MÁTICS (2003) greater wandering only happens during the youth-year and later no more.

In table 9 it was striking that the part of pair partners of the same age in all age classes was clearly higher as could be expected at hazard (table 8). It seems possible that pairs with the same or a similar age longer remain faithful to each other and/or that at new pairing a similar age is preferred. This indeed already had been reported from the analysis of the data from the Lachendorf population (KNIPRATH 2007: 26/27). That in the faithful pairs only 54.55% of the partners belong to the same age group against 67.64% of all pairs as well indicates that Barn Owls preferably chose mates of the same age group. As to the breeding success (see below) we didn't find any indication that the combination of mates of the similar age group was of advantage.

When mating for the first time as yearlings the ♀ on average find a mate slightly older than the ♂ of the same age (table 10), both indeed an older one (nothing else is possible!). Correspondingly the new mates of the remaining age groups and also of

both sexes mostly are about one year younger. If we follow EPPLE (1985) in assuming that the more agile ♀ sooner chose than the ♂ (breeding site owner), we could conclude that the preference of the ♀ for a certain age would change after the first brood as yearling. Such a changing of the preference indeed is not necessary. As yearling the ♀, despite of an inherent preference, cannot chose a younger mate, for it doesn't exist.

4.4 Correlation of the phonologic date of the broods

Above we ascertained that high numbers of breeding pairs on one hand depended on an at least mean breeding success the previous year and on the other hand on a favourable prey situation during the winter season. These two as well caused that a higher portion of the young of the preceding year reached the breeding period: There from again results the higher part of yearlings among the breeders (fig. 41) (and so the lower mean age of the breeders, at least for the ♀; figs. 37 & 38), as it was counted for years with an increased number of breeding pairs. The same was true for the population around Lachendorf (KNIPRATH 2007: 23).

Above (fig. 29) we demonstrated that the earlier egg laying (KNIPRATH et al. 2008) has not continued in the data presented here (rather improbable) or has been hidden by the strong oscillations of the values between the years. These oscillations depend on the prey situation during early springtime and the mean age of the breeders: Older ones begin earlier in the year with their brood (fig. 43). In BAUDVIN (1986: 53) in figure 24 for the years 1972-1979 no alteration can be detected.

The reduction of clutch size with ongoing egg laying date as depicted in fig. 35 in its tendency agrees with that communicated by BAUDVIN (1986: 65) and TAYLOR (1994: 160), but by no means has the extent as there. Following the trend line in BAUDVIN, the mean decreases until mid June from 7 to below 4, in TAYLOR from 5.8 below 3 (deduced from fig. 11.6a), here indeed only from 7.4 to below 6. Within the individual years TAYLOR calculated a reduction from below 8 to 3 (from fig. 11.6b). SCHÖNFELD & GIRBIG (1975: 285) indeed for most of the years found an increasing and traced that to the increasing population of the field vole towards summer.

The decrease of the elevation success with ongoing egg laying date (fig. 36) in a similar magnitude is also described by BAUDVIN (1986: 74). The markedly uniform value for the total balance in fledged young for different clutch sizes (fig. 26) as well is found in BAUDVIN (1986: 80). From the data in figure 6 in GRAEF (2004) the value of as well around 75% (like here for first broods; table 2a and fig. 26) for the elevation success can be calculated, but with distinctly increasing tendency with increasing clutch size. The original data of ALTMÜLLER gave a value of 79.5%. Hereto we should add that the first control of the broods by protection reasons was realized only very late. So, first losses of eggs and very small young, could have evaded. In both cases we have an exclusive nest box population. In BAUDVIN we find a value of 65%, also in SCHÖNFELD & GIRBIG (1975: calculated from the values in table 16) of 60%, and in JOVENIAUX & DURANT (in BAUDVIN 1986: 82) of 64.5% and so very close to the value calculated here for the total of broods (table 2). If we don't like to see herein a difference in the efforts of the owl parents, it could be a difference in the prey situation. It seems to be more likely that the owls studied by these authors exclusively breed freely (mostly in church towers) and so suffered from clearly higher losses than the nest box breeding owls in the present study and in that of GRAEF (2004). In this

connection the result of KLEIN et al. (2007) seems interesting that Barn Owls hatched in nest boxes during their later life have a significantly lower life expectancy than those elevated in free broods. The advantage of nest boxes up to fledging of the young thus later would be lost again.

The balance of the breeding success is composed (besides the dependence on the actual prey situation) of the success in producing a clutch, the performance during the incubation, the brooding, and the elevating phases. Here not only the age steps of the breeders were successful in a differing extent (figs. 45-54), but there was also an influence of the age combinations of the sexes (figs. 58-61). The yearlings had the greatest egg numbers (fig. 51), during the incubation phase the values narrowed, but indeed the old ♀ were the most successful ones (fig. 52), and during elevation the success of the old ones both sexes increased (fig. 53). In the result the old breeders of both sexes were the clearly most successful ones (fig. 54). For this not the values of all known breeders had been compared, but only those of pairs. By that, the relation between the age groups only scarcely has been influenced. The comparison with the earlier analysis of the data of the population around Lachendorf 1972-1992 (Kniprath 2007: 29-32) indeed shows differences in details: Especially also here the yearlings had been very successful in producing eggs, but the old ♀ narrowed them very closely. During the incubation phase and also during elevation the respective medium old owls were the better ones. There this was also true for the balance. An indeed different picture was found for the combinations of the age groups: Here for the clutch size the medium old ♂ were most successful together with old ♀. During the later breeding phases the combination old ♂ with yearling ♀ clearly projects, followed by old ♂ with similar old ♀. In balance we found the same valuing. In the earlier study (Kniprath 2007) there is no accordance with this. Reasons for that are unknown.

Different from the result here (fig. 51) SCHÖNFELD & GIRBIG (1975: 286) are convinced that the age of the breeders (only ♀ considered) has no influence on the clutch size. Indeed, this statement only was based on five ♀ with altogether 18 broods. TAYLOR (1994: 286) at least states that ♀ yearlings do not lay significantly fewer eggs than the ♀ of other age groups.

4.5 Pairs

The selecting behaviour of Barn Owls of different ages already has been studied earlier (Kniprath 2007: 27). There unfortunately the time scale differing one year between former and new mates not has been considered, what indeed is necessary. The table there (7) is corrected and now given here as number 13:

	Jährlinge		mittelalte			alte		
	n	neuer Partner	n	vorheriger Partner	neuer Partner	n	vorheriger Partner	neuer Partner
♂	13	1,48	28	2,93	2,61	9	5,7	3,33
♀	8	1,42	16	2,98	2,55	7	5,31	3,43

Table 13: Mean age of former and new mates after change (corrected after KNIPRATH 2007: 27, table 7)

Compared to this table the values in table 9 here not are generally different, but the differences in part greater. The mates of the ♀ yearlings are clearly older and those

of the medium aged ones younger. For the old owls the basing values of the preceding partners are clearly lower and there for also the differences against the now mates smaller. For an all together about twice as great number here, the part of old breeders seems to be lower.

MÁTICS et al. (2002) for Hungarian Barn Owls came to the same conclusion as here (tables 11 & 12) that the plumage colour doesn't play a role in mate choosing. ROULIN (1999) on the contrary had found such an influence in Swiss owls. Of course, in that study the under part spottiness of the ♀ and not the under part coloration of both sexes had been measured.

Acknowledgements

About 40 volunteers, among them five over the total time of the study (HANNA LNGE, SABINE STAHL, GUNHILDE STEFFENS, HARTMUT AHRENS, und FRANK SCHOMBURG) , have made possible this study by their engagement at nest box controls and box cleaning. We thank them all for their help.

As well very helpful for the execution of the study was that many building owners had allowed us to enter their properties unannounced all days as well as over night. Of other buildings we had a key. As after some years the "owl-car" not only was well known to all house owners but also to their neighbours, we only in one night experienced the friendly (indeed, not ironically) visit of policemen.

The number of ladders given to us, which could stay at the owl boxes over the years, summed to >100. That as well increased the velocity at control and cleaning activities. Some owner constructed plate forms in front of the boxes and so facilitated our work and made it safer.

The authorities of the county Northeim during the majority of the years made additional helpers at our disposal for posting and hanging down of boxes as well as for manifold activities in this connection. Also all the material for the construction of these boxes and their construction itself was payed by the county.

Further we experienced again and again manifold support and help. We wish to thank them altogether.

The drs. Hugues Baudvin and Bernhard Kaupe thoroughly read the paper. I wish to thank them for valuable comments and proposals.

5 Summary

This study was carried out in the years 1996-2010. The study area was the northern area of the Rural District of Northeim in southern Lower Saxony with the five boroughs of (from W to E) Dassel, Einbeck, Kreiensen, Bad Gandersheim, and Kalefeld between approx. 9.6° & 10.1° O and 51.75° & 51.9° N.

Despite the relatively small differences in altitude within the study area (max. 350 m; areas free of wood up to 250 m), the breeding sites proved to be altitude-dependent with the lowest areas at around 90-160 m above NN being very clearly preferred. It was found that a certain selection of breeding sites took place, both in the case of first breeding by new recruits and of site-changes.

The Barn Owl population of the study area breeds almost completely in nest boxes, of which around 310 were installed in about 100 villages. Even in the best breeding year (2005), only around 100 nest boxes were occupied. Even though Kestrels nested in up to 100 of the boxes, the Barn Owls thus still had a choice of sites. Boxes

installed in church steeples were occupied relatively less frequently than the other boxes. The owls thus showed no particular preference for the higher locations.

The number of breeding pairs, dates of first egg laying, the size of clutches and the breeding success vary from year to year, but not synchronously. The presumed reason for this is the fact that the size of the micro rodent population (particularly that of the common vole) also fluctuated within any one year, and that this fluctuation did not always follow the seasons. The individual years of the study are characterized in accordance with these factors.

The proportion of own-bred recruits, at 28.57% in the case of ♂ and 15.25% in the case of ♀, was significantly lower than in a comparison population. Reasons are stated for regarding immigrants as first-year birds and therefore including them in the analysis.

Of the evaluated total of 520 broods, 79.6% were successful. 80% of the breeding females and 79% of the breeding males were checked. Both ♂ and ♀ showed preferences for particular areas and also for particular boxes. In this selection, the ♀ were more successful than the ♂, older birds were more successful than first-year birds and immigrants were less successful than birds that had changed breeding site within the area.

Young ♂ originating from higher-ranking locations clearly enjoyed an advantage with settling near to their place of birth, but not with finding a higher-ranking breeding site. However, those ♂ which hatched earlier in the year enjoyed advantages in both cases.

On average, breeding females were younger than breeding males. The average age of breeding birds was somewhat lower in years with more broods because of the higher proportion of first-year birds. In the case of checked broods, the distance to the place of origin of the ♂ was, on average, half as long as in the case of ♀. Data on nest site faithfulness are provided.

Early clutches normally contained 6-7 (8) eggs. Clutch sizes decreased as the breeding season progressed. The success rate (number of fledged young per 100 eggs) of clutches containing up to 10 eggs was quite uniform, at 75%. (In the case of non-nest-box breeders in earlier studies, it was approx. 10% lower.) The success rate declined very uniformly and distinctly in line with the date of first egg laying.

Differently to an earlier study, no trend could be distinguished in the date of first egg laying over the years. In line with the age of owls of both sexes egg laying began later.

First-year birds were more successful as regards the clutch size, while the middle-aged and old owls were more successful with breeding and attending to the young. In addition to the different performance of the age groups, there were also differences in success between different age-combinations within individual pairs.

In the formation of new pair bonds, the genders showed different rates of success, depending on whether they remained at their previous location or moved away. The measure for this was the lifetime production of fledged young. In mate selection, a

certain preference for an identically aged partner was noted, but there was no preference for identical colouration.

Literature

ALTMÜLLER R 1980: Eine Methode zum Fang von Schleiereulen. Vogelwarte 30: 333-334

BAUDVIN H 1986: La reproduction de la Chouette effraie (*Tyto alba*). Le Jean le Blanc 25: 1-125

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

EPPLE W 1985: Ethologische Anpassung im Fortpflanzungssystem der Schleiereule (*Tyto alba*). Ökol: Vögel 7: 1-95

GRAEF K-H 2004: Bestandsentwicklung, Brutbiologie, Dismigration und Sterblichkeit der Schleiereule *Tyto alba* im Hohenlohekreis (KÜN)/Nordwürttemberg. Ornith. Jh. Baden-Württemberg 20: 113-132

HERRMANN W, HERRMANN I & APEL R 2010: Ergebnisse zehnjähriger Untersuchungen an der Schleiereule (*Tyto alba* SCOPOLI, 1769) in der Umgebung von Dessau (Sachsen-Anhalt). Naturw. Beitr. Mus. Dessau 22: 157-162

JAHNEL M 1989: Brutbiologie und Wanderungen einer Schleiereulenpopulation (*Tyto alba*) im hessischen Main-Kinzig-Kreis. Luscinia 46: 165-181

KLEIN Á, NAGY T, CSÖRGÖ T & MÁTICS R 2007: Exterior nest-boxes may negatively affect Barn Owl *Tyto alba* survival: an ecological trap. Bird Cons. Int. 17: 263–271

KNIPRATH E 2007: Schleiereule *Tyto alba*: Dynamik und Bruterfolg einer niedersächsischen Population. Eulen-Rundblick 57: 17-39

KNIPRATH E 2011: Scheidung und Partnertreue bei der Schleiereule *Tyto alba*. Eulen-Rundblick 61: 76-86

KNIPRATH E 2012: Die Wanderung nestjung beringter, norddeutscher Schleiereulen *Tyto alba* nach dem Material der Vogelwarte Helgoland – Teil 1. Eulen-Rundblick 62: 101-110

KNIPRATH E 2013: Die Wanderung nestjung beringter, norddeutscher Schleiereulen *Tyto alba* nach dem Material der Vogelwarte Helgoland – Teil 2. Eulen-Rundblick 63: 30-46

KNIPRATH E & STIER S 2006: Zur Unterseitenfärbung einer Population der Schleiereule *Tyto alba* „guttata“ in Südniedersachsen. Vogelwarte 44: 233-234

KNIPRATH E & STIER S 2008: Schleiereule *Tyto alba*: Mehrfachbruten in Südniedersachsen. Eulen-Rundblick 58: 41-54

- KNIPRATH E & STIER-KNIPRATH S 2010: Schleiereule *Tyto alba*: Jungvogel an Geschwister verfüttert. Eulen-Rundblick 60: 66-68
- KNIPRATH E & STIER-KNIPRATH S 2011: Schleiereule *Tyto alba*: Zu den Umständen eines Partnerwechsels für eine Zweitbrut. Vogelwarte 49: 75-77
- KNIPRATH E, WUNTKE B, SEELER H & ALTMÜLLER R 2008: Verfrühung des Legebeginns bei der Schleiereule *Tyto alba*. Vogelwarte 46: 37 – 38
- MÁTICS R 2003: Direction of movements in Hungarian Barn Owls (*Tyto alba*): gene flow and barriers. Diversity and distribution 9: 261-268
- MÁTICS R, HOFFMANN G, NAGY T & ROULIN A 2002: Random pairing with respect to plumage coloration in Hungarian Barn Owls (*Tyto alba*). J. Ornithol. 143: 493-495
- MEBS T & SCHERZINGER W 2000: Die Eulen Europas. Kosmos
- ROULIN A 1993: Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. Behav. Ecol. 10: 688-695
- ROULIN A 2004: The function of food stores in bird nests: observations and experiments in the barn owl *Tyto alba*. Ardea 92: 69-78
- ROULIN A, DIJKSTRA C, RIOLS C & DUCREST A-L 2001: Female- and male-specific signals of quality in the barn owl. J. Evol. Biol. 14: 255-266
- SCHÖNFELD M & GIRBIG G 1975: Beiträge zur Brutbiologie der Schleiereule, *Tyto alba*, unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte. Hercynia N.F. 12: 257-319
- TAYLOR IR 1994: Barn Owls. Predator - prey relationships and conservation. Cambridge Univ. Press