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Barn owl *Tyto alba*: Multiple breeding in Southern Lower Saxony, Germany

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Key words: barn owl, multiple breeding, breeding strategies, bigyny, distribution of resources hypothesis

Content

Introduction
There is hardly any paper on the breeding biology of the barn owl in Europe not merely mentioning that under favourable circumstances this species elevates more than one brood per year. At free broods mostly in church towers BAUDVIN (1979, 1986) and MULLER (1999) intensively collected and studied data. MULLER mostly focussed at the phenomenon at the level of the species, BAUDVIN by ringing adult birds additionally stressed the role of the latter ones. Data concerning ethological questions in connection with multiple breeding are found in EPPLE (1985). The tendency or barn owl to breed more than once per year led to the assumption of a year round breeding preparedness. In a box population in Southern Lower Saxony, Germany, we succeeded to control >80% of the breeders. The data thus obtained promised more detailed insights into the phenomenon multiple breeding in this species.

2. Material and methods

From 1996 to 2006 in the eastern forelands of the Harz Mountains (9.87E , 51.82N) the breeding adult barn owls and their chicks were ringed (with rings of the Vogelwarte Helgoland). All broods took place in boxes. The amount of boxes oscillated around 300 with a mean number of about three boxes per village (N=99). Free broods are nearly unknown. Among the totally controlled broods there were only three, one of them unsuccessful, the parents and the young of the second one could be ringed. Twice we fond an very strong suspicion for a brood outside the boxes. All conclusions made here exclusively base on ringed owls. For this study we use 435 broods. The amount of controlled breeders is 82,8% (♂: 79,5%; ♀: 86,0%). Except in one free brood not controlled and one in a box not accessible the young of all broods could be ringed. So breeders caught without ring at more than 99% were immigrants. To test significance of differences between mean values we used ANOVA as integrated in MS Excel. Significance threshold was at $P <= 0,05$.

2.1 Definitions

Overlapping broods

These broods do not represent a special category of broods but only a characteristic form of temporal organisation. For barn owls authors published a period of about 100 days from egg laying to fledging (EPPLE 1985, BRANDT & SEEBAß 1994, GLUTZ VON BLOTZHEIM & BAUER 1994, SCHNEIDER & ECK 1995). (Even thereafter the fledglings are depending on (additional) feeding by their parents.) Then a normal second brood may follow. But barn owls do not always wait as long but sometimes considerably earlier start laying again (EPPLE 1985, MULLER 1990, GLUTZ VON BLOTZHEIM & BAUER 1994: 255). Since SCHUBERT (1959, cited in ALTMÜLLER 1976) German authors name these overlapping broods "Schachtelbruten". (Correctly we should speak of "Schachtel- Zweitbruten" meaning overlapping second broods.) In each type of overlapping broods the ♀ renders all further elevation of the young to the ♂ alone (ROULIN 2002). As usual also in overlapping second broods the ♀ incubate beginning with egg one. So they never are engaged in two broods simultaneously.

Second / third brood

Following BAUDVIN (1979, 1986) and MULLER (1999) we here only name those broods second broods which are preceded by a successful first brood with at least one fledgling or in which a first brood still had been existing at the beginning of the second one. So only broods which were preceded by two successful ones may be called third broods. This definition easily may be used in second or third broods of pairs but not if only one mate of the first brood is engaged in a further one or both mates in different further ones. As "partition second broods" is not precise enough we here use the term "second-brood-index". This means the partition of spring broods (in %) which is followed by a second brood.

Replacement brood

Again following BAUDVIN (1979, 1986) and MULLER (1999) we do not name those broods second broods which follow an unsuccessful one. But as they are second **attempts** as well we include them here.

3. Results

Like the total numbers of broods those of multiple breeding attempts heavily oscillate from Year to year (fig. 1). Here we only use spring broods (first half of the year, N=347) as a basis, because among those of the second half of the year (N=88) we mostly find broods which should be studied in their relation to those of the first half of the year. If all broods of the second half of all years are counted as second broods (as most authors do) the second-brood-index would be 25,4%.
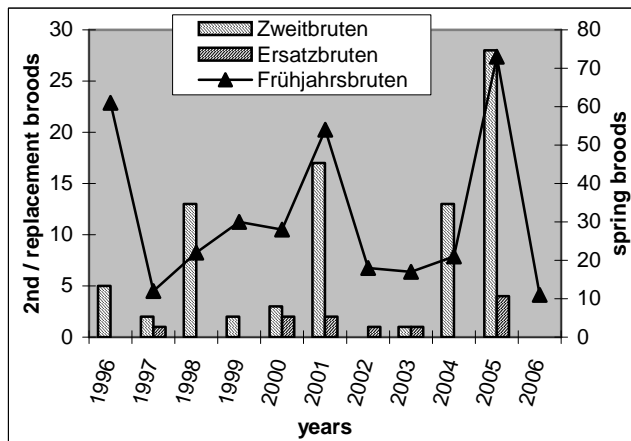

Figure 1: Second (Zweitbruten) and replacement broods (Ersatzbruten) in relation to the total numbers of spring broods (Frühjahrsbruten)

3.1 Second broods
In the sense defined above we altogether found 74 second broods, i.e. as a mean 21,3% of the first broods of a year we followed by a second one. In years with decreasing or with very low breeding pair numbers (fig. 1) they were extremely rare. Years of a +- considerable increase of the population always were such with second broods. Stagnation of pair numbers at a high level did not occur in the study period. The numbers of second broods increased with the numbers of spring broods (fig. 2), but the correlation is not close. The correlation is much more evident between the second broods and the amount of the alteration of the brood numbers against the preceding year (fig. 3). Taking only the four years with many second broods (1998, 2001, 2004, 2005; in the following called "success years") the first broods are followed by only 65 broods in the second half of the year (as possible second broods). Already this relation (index 38,2%) clearly indicates that even in these years by far not all first breeders make a second attempt. The index of proven second breeders (N=71: some second breeders already start in the first half of the year) in these years reaches a mean of 41,8%, hence is higher than the estimation (38,2%).

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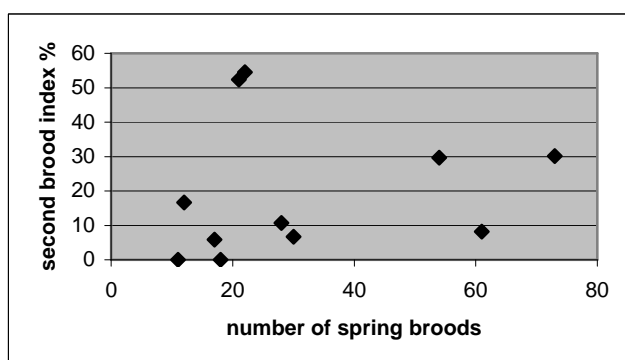
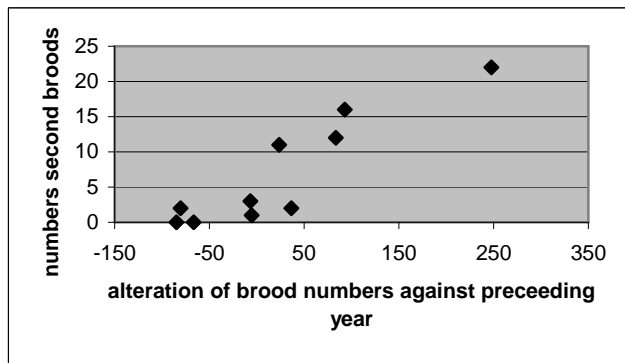Figure 2: The correlation between the numbers of spring broods per year and the index of second broods

Figure 3: The correlation between the numbers of second broods and the alteration of the spring brood numbers against the preceding year

Years with second broods mostly were years with higher egg numbers but rarely with higher numbers of fledglings. As a mean clutch size in years with second broods (first half of the year only) was 7,0 (N=134), in those without 6,2 (N=151) (P<0,001 ANOVA); fledgling numbers respectively 4,7 against 4,4 (not significant (ns) ANOVA).

Of the altogether 421 breeders controlled (228 ♀, 193 ♂) at all 87 (20,7%) (39 ♂: 20,2%, 48 ♀: 21,1%) were engaged in second broods. One ♂ had 3, 2 ♂ had 2 each, and the resulting 33 only one second brood each. For the ♀ the respective numbers are: 2x3; 5x2; 41x1. During the success years in the spring broods 306 breeders were controlled (157 ♀, 149 ♂). Later 38 (25,5%) ♂ and 45 (28,7%) ♀ of these bread for a second time. These numbers are considerably lower than the 38,2% of the estimation above.

The intuitive assess: "early egg laying – many second broods" only in part is confirmed by figure 4. More likely it becomes visible that a late egg laying (after day 115, that means April 25) scarcely makes expect second broods. Early egg laying also may coincide with very few or totally lacking second broods. For information whether the second breeders themselves, which mostly were found in years with early egg laying, were already earlier first breeders, see beginning of chapter 3.2.
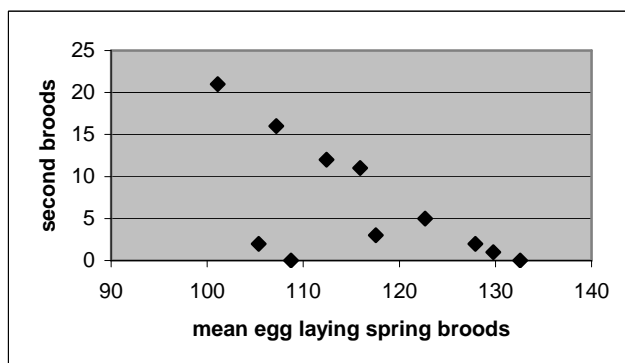

Figure 4: Correlation between mean egg laying (days after New Year) and number of second broods each year

We may assume that at sites with generally many broods also second broods may be more numerous than at other sites. Fig. 5 of course demonstrates that there is no general correlation of relative numbers.

Figure 5: The frequency of second broods in dependence on the number of spring broods per village (N=49)

The broods of the first half of the year (N=134; only success years) had a mean clutch size of 7,0, those of the second half (N=49) of 7,6 (ANOVA: P=0,07). This difference is not significant. If comparing only recognized first to second broods the mean value of the 138 first ones is 7,1, that of 84 second ones 7,5 (ANOVA: P=0,1). This difference which in numbers is still smaller is not significant. If we then compare the real success in fledgling numbers, the result is clear: The mean values of the halves of the year (4,7 resp. 3,5; P<0,01, ANOVA) and those of first and second broods (5,3 resp. 3,8, P<0,001, ANOVA) not only differ significantly but have inversed in their relation: The second as well as the autumn broods in general had evidently less success. A next comparison likewise demonstrates the inferiority of the autumn broods: 78 (5,2%) of the fledglings of the first half of the year (N=1496) but only 22 (3,6%) of those of the second half (N=606) were again controlled during a following year.

The result per year of all birds breeding twice in the second brood years (mv fledglings: 9,3; N=48) of course was evidently superior to that of birds having bred only once (mv fledglings: 5,5; N=68; P<0,001 ANOVA). For comparison within the double breeders see chapter 3.2.

A more exact examination of the second broods demonstrated that there were different categories. In 30 of the second broods (=40,5%) the pair of the first brood also realized the second one in common. There were 13 more ♂ and also 13 ♀ (together 35,1% of the second broods) with a second brood but with a new mate. For the rest of the broods in the second halves of the years there was not enough information for the judgement or already in the corresponding first brood we don't know both mates. So these no more are considered.

3.1.1 Second broods of pairs
For all 30 second broods of pairs the egg laying for both, first and second broods, are known or were calculated. The time interval between these two oscillated between 69 and 113 (twice) days, mean value 92 (fig. 4). Basing on the duration value (100 days) of a normal brood (as fixed under the point "overlapping") >50% of these broods overlapped. The time intervals between first and second broods do not seem to be dependant on the egg laying of the first brood (fig. 5).
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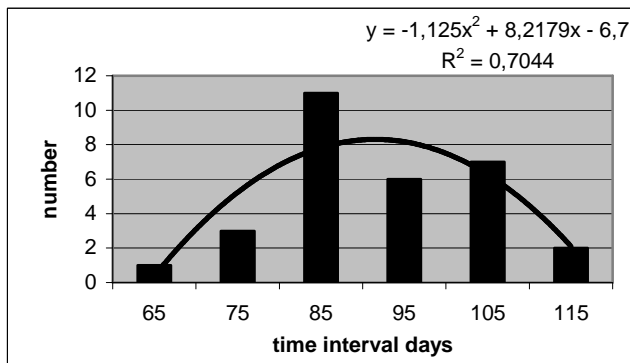
Figure 4: The time intervals between first and second broods in 30 double breeding pairs (N=30)
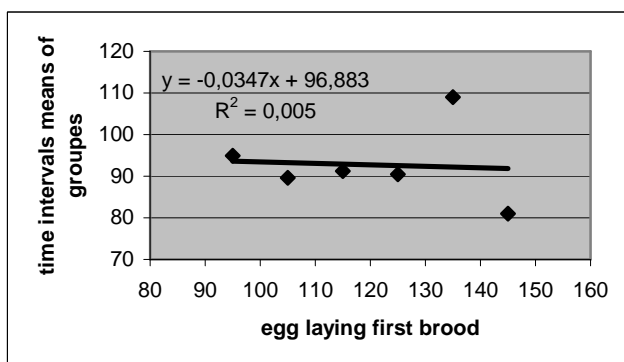

Figure 5: The dependence of the time intervals between first and second broods on egg laying of the first brood (30 double breeding pairs)

Only three of the double breeding pairs stayed in the box of the first brood. The predominant majority selected a box in the proximate surroundings, mean at 190m (min 1; max 500m). Only one pair resettled 1,3km apart.

Seven of the ♂ involved were yearlings, 15 more than one year old, and 8 were immigrants of unknown age, presumable mostly yearlings too. The numbers for the ♀ are: 5 – 8 – 17.

For breeding success of the double breeding pairs see in 3.2.

3.1.2 Second broods of ♀ with new mate
In the 24 double breeding ♀ (without second broods as pairs) there were 13 with a new mate and both egg laying dates being known. Overlapping here was observed in a similar extend as in the second broods of pairs (fig. 6). Up to a time interval of about 100 days (N=8) that means: All ♀ had deserted their first brood and consequently their first ♂ in favour of this second brood. So at least these broods after KNIPRATH et al. (2004) must be named divorce second broods. All these deserted broods (N=8) were successful (mv fledglings 6,3), the following second broods of the same ♀ considerably less (mv 4,8) (ANOVA: ns).
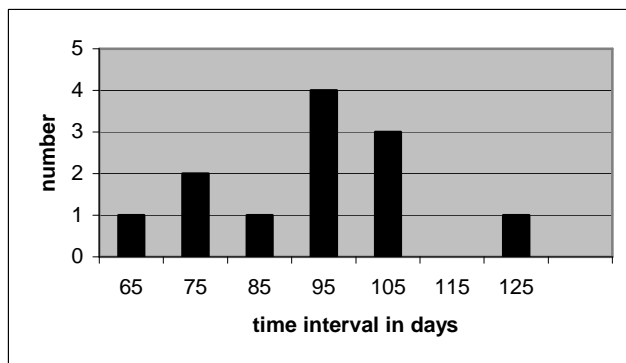
Figure 6: Time intervals between egg laying of first and second broods in 13 ♀ with new mate for the second brood

This part of the second broods too war found in the success years: 1998 1x, 2001 1x, 2003 1x, 2004 6x; 2005 4x.

None of these second broods occurred in the box of the first brood, even not that one with the time interval of 121 days. If the maximum value of 89 km is not considered, the second broods took place at distances from 0,2 to 13,7km (mv 4,3). Although we had supposed, there was no indication for a correspondence between these distances and the time intervals between the corresponding two broods.

In one of the belonging first broods we found a faithful pair of the preceding year. A second pair was the same as in the spring of the preceding year but the ♀ had inserted a divorce second brood. Two more ♀ had lost their mate of the preceding year, one had remarried the divorced mate from three year before. One was a yearling and the remaining eight hitherto unknown (immigrants).

Three of the ♂ of the first broods were breeders of the preceding year which had lost their mates. Four were yearlings and the rest unknown. One ♂ of the second broods was yearling, 4 more known breeders of the preceding years and 8 until then unknown immigrants.

For three of the ♀ the further fate is known: one has lost here ♂ and had moved, one deserted her ♂ and moved, and the third ones was faithful. Fife of the ♂ of the first broods stayed at their breeding site despite of the loss of their ♀ and found a new one. To a further one the ♀ came back after a divorce second brood and bred again with him the year after. All other fates are unknown. Five of the seven ♂ of the second broods with known fate lost their ♀ thereafter, one by divorce, all others probably by death. Four of these seven stayed and three moved. One ♀ was engaged in two consecutive years in divorce second broods.

3.1.3 Second broods of ♂ with new mates
Among the 13 second broods of ♂ with new mate (12 of which with known egg laying) there were – as in the double breeding pairs and the ♀ with a new ♂ - overlapping and not overlapping ones (fig. 7). But in contrast the lower part of the time intervals between the egg laying of the two broods was much lower (2x 15 days) than in these two (see fig. 4: not lower than 69 days). Additionally there was a considerable time gap between overlapping and not overlapping broods. The not

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overlapping broods are normal second broods. Those which were overlapping at a considerable amount normally are named bigyny.
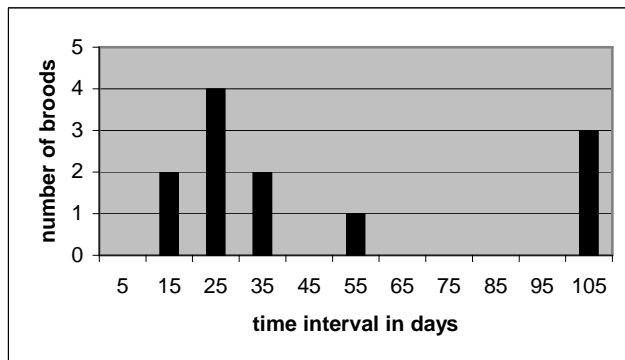

Figure 7: Time intervals between egg laying of first and second broods in 12 ♂ with new mate at the second broods

Bigyny
The ten cases of bigyny (nine of them with sufficiently known data) exclusively were found in the years with highest numbers of second broods: 1x 1998, 1x 2001, 2x 2004 und 6x 2005 (see fig. 1). These were years with a considerable increase in pair numbers. The egg laying of the belonging first broods had a mean value of day 106,9 versus 107,2 of all first broods of the same years. These mean values will be discussed in common later.

Two each of the first and second ones of these brood were unsuccessful, one of each of these was deserted during the clutch stage. Judged as well by clutch size (mv 6,3 resp. 6,4) as by fledgling numbers (3,7 either), the ♂ invested similarly into their two broods. Altogether they were more successful (by fledglings) than the ♂ which had no second broods (mv 7,3 versus 5,5; P=0,01, ANOVA), but less than those ♂ producing a second brood with the ♀ of their first brood (mv 10,2; P<0,01, ANOVA).

The distances we found between the respective breeding sites were from 50m (second box in same building) and 3,2km (mv 1,1km).

For four of the 10 ♂ concerned the exact age is known (2x 1, 1x 2 & 1x 4, mv 1,75 years), for further three the minimum age (1x 2, 2x 4, mv 3,3 years). The remaining three hitherto were unknown. Five of them had been breeders already the preceding year, two were own yearling recruits.

Six of the ♂ were no more recovered later. One, *Conrad*, the year later made one more brood with the ♀ of his bigynic second brood and two years later to more broods with her. *Leo*, whose bigynic first brood with *Otti* had been deserted during clutch stage, after the end of his bigynic second brood with *Okarina*, made a normal second brood (interval: 103 days) with *Osithe*. Of course we could also classify this one as replacement brood (for the first one with *Otti*). However, three different ♀ were engaged in the three breeding attempts of *Leo* in one single year. The third ♀, *Osithe*, hitherto had been unknown. Following her unsuccessful bygynic first brood *Otti* at a distance of 1,3km made a replacement brood with a new ♂ (own recruit from the preceding year). As at that time *Leo* was still living and had his own brood, a divorce had preceded (following unsuccessfulness?).
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In a further ♂, *Odysseus*, the development was similar: After desertion of a bigynic second brood with *Ophelia* during clutch stage, at the distance of 150m a further, successful brood was made with *Orschel*. The egg laying interval between the latter one and the successful bigynic first brood of *Odysseus* with *Ota* was 92, and to the unsuccessful bigynic second one with *Ophelia* 77 days. So it can be understood as replacement brood for the latter ones, in any case as second brood. *Orchel* in this case made her regular second brood.

As there was no bigyny with both broods successful, and additionally one more brood of the ♂, even that way no third brood was established.

Three of the 20 ♀ were own recruits from the preceding year, 13 unknown so far, the remaining four breeders of the preceding year (1x 2, 2x 3 & 1x 4 years at least old respectively). Fourteen were no more recorded after. Five were present thereafter as breeders for at least one year, one of these one year with the same mate. The remaining owl is *Otti*, the bird already mentioned with replacement brood after divorce.

Four of the ♀ were unsuccessful, two of these not recorded further on. One more – after divorce – made a replacement brood with a new ♂ (see above). For the fourth ♀, *Karsta*, the development will be depicted in more detail as she was engaged in two bigynies. In the first year (ringed with unknown age) she was successful bigyny first- ♀. After two more years (successful in the second one) she then in her fourth year was unsuccessful bigyny first-♀, and disappeared thereafter. So she had four breeding attempts of which two were successful.

These detailed descriptions of the cases observed possibly allow to recognize an accumulation at one detail: More than one half of the ♀ engaged are immigrants and therefore possibly yearlings. If we add those that certainly are yearlings, the partition of inexperienced birds reaches up to 80%. In the ♂ we find at least 50%. (For partition numbers in the total of breeders see table 2.)

Second broods, not bigyny
The three cases with a time interval of the egg laying of more than 100 days from the first brood here are classified as regular second broods, even if the ♂ during the new display behaviour still for some time were engaged in foraging the young of the first brood. One of the ♂ was known as breeder of the preceding year, the two others were unknown. All three ♀ of the first broods hitherto were unknown as well as those of the second broods. For more details of these broods see at 3.2.

3.2 The strategies in comparison
In chapter 3.1 we stated that years with early mean egg laying of the broods of the first half of the year only limited were those with exceptionally many second broods. Here we add the question whether those individuals which are engaged in any kind of second brood generally have other first brood data than those who do not. To compare we only used data from the four years with a clear amount of second broods: 1998, 2001, 2004, and 2005. We had 60 first broods followed, and 68 not followed by a second brood with sufficiently enough data for comparison at our disposition. Here the image was unexpected: The double breeders started two days

later. The mean values of the egg laying of the spring broods are: day 103,5 (without second brood) resp. 105,1 (with); indeed the difference is not significant (ANOVA). The mean values for clutch size are very similar: 7,05 and 7,2 eggs (ns: ANOVA); the numbers of fledglings are identical: 5,48. The later second breeders really invest as much into their first brood as those owls, which produce only one brood, into this latter one.

We could also suggest that there were two different life strategies: (1) to breed with full power as long as circumstances are favourable or (2) to save energy and to count for a next breeding year. Condition for this second variant should be a favourable survival rate. It seemed to be possible that preservation would better survival chances. Examination of the real survival rates in the population again surprised: double breeder reached the following breeding season with a remarkably higher probability (23,5% versus 13,2%) than individuals which bred only once. With any caution we might deduce that breeding twice a year probably is no question of strategy but attached to the total quality of the individuals. All values found, arranged by sex, year, and breeding strategy are in table 1. There may be remarked that of the many double breeders in the years 2001 no ♂ survived and also of those of the year 2005 none was recovered in 2006. This latter is also valid for the double breeding ♀ 2005.

Table 1: Survival rates by sex and breeding behaviour in the four double brood years

| | males | | | | | | females | | | | | |
| | double breeders | | | single breeders | | | double breeders | | | single breeders | | |
year	N	surviving	part	N	surviving	part	N	surviving	psrt	N	surviving	part
1998	8	5	62,5	6	3	50,0	9	2	22,2	6	1	16,7
2001	11	0	0,0	24	7	29,2	13	2	15,4	24	3	12,5
2004	6	6	100,0	6	1	16,7	10	5	50,0	6	1	16,7
2005	14	0	0,0	32	1	3,1	14	0	0,0	32	1	3,1
sum	39	11	28,2	68	12	17,6	46	9	19,6	68	6	8,8

This interpretation by inspection indeed is strongly shocked by a chi^2 test. The alpha as well in the ♂ (31,1) as in the ♀ (15,0) is evidently outside the range of significance (limit 5,0). But as the combination of the values of the sexes leads to an alpha of 10,1 and so approaches the threshold we could guess that greater material still could show significance.

Ages of the participants
Age and experience of the breeders and also their knowledge of the conditions in the surroundings of the breeding sites could influence their decision to add a second brood or not. For examination three age groups were introduced for each sex: yearlings, older ones (>1 year) and immigrants. Table 2 demonstrates, that there really differences could be detected. Only in the older breeders, in the ♀ even clearer than in the ♂, the part of those who breed twice is higher. We deduced with caution that age and/or experience might stimulate readiness to breed twice. In the ♂ the values of the immigrants are between those of the yearlings and the older birds, in the ♀ they do not.

Table 2: The partitions (%) of breeders with or without second broods, separated for sexes and age groups (and immigrants) (N)

	males		females	
	double breed.	single breed.	double breed.	Single breed.
aged	54,35 (25)	45,65 (21)	67,74 (21)	32,26 (10)
yearlings	40,63 (13)	59,38 (19)	42,11 (8)	57,89 (11)
immigrants	44,00 (22)	56,00 (28)	39,74 (31)	60,26 (47)

The chi2 test first confirmed that within the ♀ somewhere there is a significant difference (alpha = 2,8) but not in the ♂ (42,8). If we omitted the immigrants (as being uncertain with respect to age) for a new test the significance also for the ♀ mostly disappeared (7,8). Perhaps the immigrated ♀ do have different qualities?

Distances of breeding sites of all second events from first breeding site
Even during the year 2005 with the highest number of breeding pairs ever recorded only about 30% of the boxes were occupied by barn owls and about the same number by kestrels. The latter ones must not be taken in account here as the young kestrels mostly had fledged at egg laying of the majority of the events discussed here. So for the barn owls there were always several free nest boxes in close vicinity for a further breeding attempt. The behaviour of the owls when choosing a site for a second breeding event is unmistakable: Among all the 80 second breeding events analysed here there were only three where the owls used the box of the first brood also for the second one. And these three were second broods of pairs. For all other second broods the owls used a different box. So we don't doubt: If in the close vicinity there is a free box at their disposition, this one nearly without exception is preferred to that of the first brood.

Including replacement broods we tested whether depending on the type of second event the owls moved at different distances. With a P<0,05 the analysis of variance made us guess that there is some difference between the means of the distances found. If we did not include a "runaway" of 89km (a ♀ coming from the ringer colleague HORST SEELER), the P is lower than 0,001. The individual tests (ANOVA) showed (tab. 3) that the differences between the 4,3km of the second breeding ♀ with a new ♂ and the 4,4km of replacement broods. Equally not significant is the difference of 1,7km of the ♂ with a new ♀ and the 4,3km of ♀ with a new ♂. All other differences are significant: Pairs stay in the closest vicinity (0,2km) for their second broods. Males with a new ♀ move a little farther (1,7km). In this comparison the cases of bigyny are enclosed. Bigyny second broods never took place in the same box as the bigyny first broods. Though the mean values differ considerably (bigyny: 2,1; second broods: 0,6km), this difference is not significant (P>0,05). A closer examination of the second broods of ♀ with new ♂ gave no indication for a connection between the alteration of the time interval between these broods and their special distances.

Table 3: The significances of the mean value differences of the distances between second events and first broods (without the "runaway"). "new" means "with new mate".

events (N; mean distance)	replacement	second br. pairs	second br. Females new
replacement broods (13; 4,4)			
second broods pairs (30; 0,2)	P<0,001		
second br. females new (12; 4,3)	P=1,0	P<0,001	
second br. Males new (13; 1,7)	P<0,05	P<0,01	P=0,1

Time intervals between first broods and second breeding events
As already presented in the preceding chapter in the most breeding pairs there are free breeding boxes. So we had not to expect that the onset neither of a replacement brood nor of a bigynic second brood of a ♂, as being the events following the closest, should be delayed by a to small offer of breeding sites.

When comparing the mean values of the time intervals of all second events we found significant differences (ANOVA). Table 4 shows that most differences between the means are highly significant, but not those between replacement broods and the second broods of ♂ with a new ♀ and those between second broods of pairs and of ♀ with new ♂: These latter ones on average follow the egg laying of the first broods after 91,7, resp. 92,8 days. For replacement broods and second broods of ♂ with a new ♀ this distance is much closer: on average 51,5 resp. 48,0 days. The latter ones mostly are bigynic second broods. If we separate these (N=9) from the normal second broods (N=3), the latter ones have an interval of 105, the former ones of 29 days.

Table 4: The significances of the mean value differences of the intervals between second events and first broods (ANOVA). "new" means "with new mate".

event (N; mean interval)	replacement	second br. pairs	Second br. Female new
Replacement broods (8; 51,5)			
Second broods pairs (30; 91,7)	P<0,001		
Second br. Females new (12; 92,8)	P<0,001	P=0,8	
Second br. Males new (12; 48,0)	P=0,8	P<0,001	P<0,001

Clutch sizes of second broods
The examination of all groups together gave a P=0,001 (ANOVA): The comparison between all single group means then showed no significant difference between replacement broods and the second broods of ♂ with new ♀ and that between pairs and the ♀ with new ♂. All other differences are significant (table 5): Replacement broods and second broods of ♂ with new ♀ (which mostly are bigyny second broods)

do have smaller clutches. This remains true even if we differ between bigynic and normal second broods. The means of these latter ones indeed do not differ (6,0 resp. 6,2). The second clutches of pairs are mostly as big as those of ♀ with a new ♂ (ANOVA: ns).

Table 5: The significances of the mean value differences of the clutches between second events and first broods (ANOVA). "new" means "with new mate".

events (N; mean clutch size)	replacement	second br. pairs	second br. females new
replacement broods (11; 6,6)			
second broods pairs (30; 8,2)	P<0,01		
second br. semales new (13; 8,6)	P=0,01	P=0,5	
second br. males new (13; 6,3)	P=0,7	P=0,001	P<0,01

Breeding success of second broods
The mean (fledglings) of second brood ♀ with new ♂ seems to be quite higher than that of all other groups (table 6). Nevertheless examination of all groups together (ANOVA) gives a P=0,4. The differences found thus are not significant.

Table 6: The significances of the mean value differences of the breeding success (fledglings) between second events and first broods (ANOVA). "new" means "with new mate".

events (N; mean fledglings)	replacement	second br. pairs	second br. females new
replacement broods (11; 4,6)			
second pairs (30; 4,2)	P=0,7		
second br. females new (13; 5,1)	P=0,7	P=0,3	
second br. males new(13; 3,3)	P=0,3	P=0,3	P=0,1

In addition to the question studies above whether double breeders are more successful than single breeders (measured as fledglings) we will show now, which concerning differences there are between the second brood strategies outlined above. The comparison of the mean values of all strategies (annual result: pairs mv : 10,6; new pairs of the ♀ mv: 11.4; new pairs of the ♂ mv: 73; bigyny only: 7,4) gives significant differences (P<0,01 ANOVA). Mean comparison between all single values elucidated that the new partnerships of the ♂ are significantly worse (P<0,01 ANOVA) as each of the other strategies, but that these themselves do not differ. Expressed biologically: The comparison demonstrates that the best strategy is to make a second brood with as pair. For the ♀ it is as successful to count for a divorce second brood. For a ♂ bigyny is a clearly worse strategy than a second brood with the ♀ of the first brood.

3.3 Replacement broods

Sixty five (16,6%) of the 337 broods with egg laying during the first half of the year which at least for one of the mates was neither replacement nor any kind of second brood remained unsuccessful. Thirty of these unsuccessful broods had no hatching success, thus ended in the clutch stage. Opposing that we found 11 (19,6% of 56) replacement broods. (For the distribution of these replacement broods over the years see figure 1.) If it really exists, the correlation between the relative amount of replacement broods of a year and that of unsuccessful ones (0 fledglings) is very small. It shows to be a little narrower if we take the lack of hatchlings as proof for failure. The correlation between the amount of unsuccessful broods and that of the all over number is very weak (fig. 8). This amount in bad years more likely is higher with a heavy scattering of the values, in better ones preferably lower.
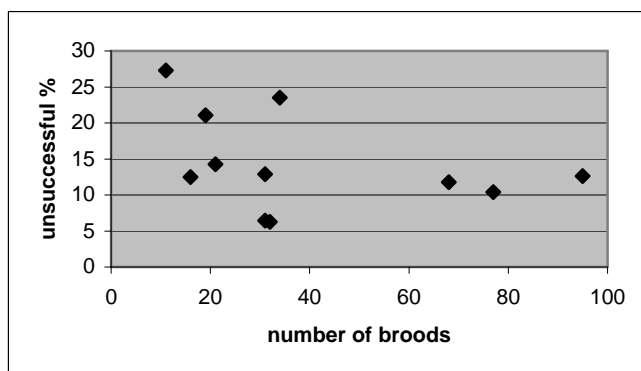

Figure 8: Relative yearly amount of unsuccessful broods

For eight of the replacement broods egg laying is known as well for this brood itself as for the replaced one. For these the time interval between them could be calculated. For the three faithful pairs it is on average 36 days (min=20; max=47), for all other second broods 62 (min=30; max=92). The conclusion is that pair are much faster to start a replacement brood. However this difference is not significant (ANOVA).

Nevertheless in none of the fatal broods the exact date of its end is known. At least for four of these we know that at the end there already were chicks (1x1,3,4,5 resp.). Mean egg laying for all fatal broods (N=44) was April 30 as well as for the broods with replacement brood (N=8). Obviously it is without importance for the probability of a replacement brood how early the fatal brood had started.

Four of the mentioned 11 replacement broods were such for both mates but only for one for the same pair. In the fourth case new partners met which both replaced their own lost brood. For further 6 ♀ we could control, the mate of the fatal brood was known only for four, and for one more even that of both broods. Five new mates not yet had been controlled that year as breeders. One more replacement brood was that of a ♂ replacing his lost first brood, a bigyny first brood. For the belonging ♀ this brood was a regular second brood. In favour of the replacement brood one of the ♀ separated from the ♂ of the first brood (divorce).

Twenty five (9♂; 16♀) of the 112 parent birds of the unsuccessful broods were known. (A considerable part of these broods were already "deserted" when found.) Fifteen (5♂; 10♀) of these made a replacement brood, 10 (4♂; 6♀) did not. Eight (4♂; 4♀) of these latter ones were recovered alive later. Possibly the lacking two ♂ could have died. For these broods the loss of a mate merely could have played a role for their unsuccessfulness.

Twenty one (10 ♂, 11 ♀) of the 22 parent birds engaged in replacement broods have been controlled. Ten ♀ and 5 of the 10 known ♂ were replacement breeders. Out of these 5 ♂ 2 were yearlings, 2 older birds, one immigrant of unknown age. Of the ♀ 2 were yearling, 3 older birds, and 5 immigrants.

None of the replacement broods was found in the box of the replaced one. The three faithful pairs on average bread at a distance of 2,9km (min 0,8; max 5,3), 6 of the ♀ on average 7,7 (min 1,4; max 9,9), one 85km (not enclosed in the 7,7km). The ♂ of the bigyny first brood (see above) had moved 5,5km, the ♂ of the pair with two independent replacement breeders 5,1km. The difference between the faithful pairs and the other replacement breeders is not significant (ANOVA).

One of the replacement broods remained unsuccessful, the mean breeding success was at 4,64 fledglings (5,1 in the successful ones). The average in clutch size was at 6,6 instead of 5,5 in the unsuccessful first breeding attempts. In these indeed it is uncertain for all those cases in which it was the clutch which was deserted, whether the clutch detected already had been a full clutch.

The interesting question whether all unsuccessful breeders made a replacement brood lead to no usable result: In fact, unsuccessful breeders which not had made a replacement brood were controlled again later in one of the following years. But there were several broods in the second half of the year in those years of failure where we did not succeed in controlling the parent birds. These could have been the lacking replacement breeders.

None of the replacement broods was followed by one more breeding attempt. In fact there were unsuccessful broods in the second half of the year (N=31), but none was replaced.

4 Discussion
Second broods of barn owls very often are mentioned in the literature. But rarely the author state whether at least the ♀ had been controlled. The majority of the indications in the literature Therefore not really can be compared. Certainly basing on ring controls are the data of SCHÖNFELD et al. (1977), BAUDVIN (1979), ALTWEG et al. (2007) and KNIPRATH (2007).

The statement here that aged barn owls more often than yearling make second broods corresponds to the results of ALTWEG et al. (2007).

For an exact analysis it proves as necessary not to name a brood as such as second or replacement brood but to estimate of every bird involved. A late brood might be a replacement one for one mate, for the other one even second or as well first brood if this one hitherto had not found an appropriate mate. As above depicted with an

example (3.1.3 under "bigyny"), a brood late in the year even for a single owl might fall under more than one category.

Neither the moment nor the site is a certain criterion for the judgment whether a particular brood is a first, a replacement, or a second one. Replacement broods for very early first broods may start earlier than some or other first brood. Likewise the start of an overlapping second brood might be earlier than that of some first broods the partners of which had met very late. A new clutch on ore above older eggs or carcasses of chicks of the same year can prove that the pair of a first brood there makes a replacement brood but must not. For an exact judgment the capture of all parent birds is necessary.

Also the supposition a late brood at the same site or in the same box "naturally" could be nothing else than the second brood of the same pair quite might be wrong. In the year 1998 in the village Hullersen (study area of the authors) three first broods were recorded. (One of these already could have been a replacement brood for at the first control in another box we fond cold eggs.) Two of them were the broods of a bigynous ♂ (*Helmut*). The pair belonging to the third brood made a second brood in one of the boxes of *Helmut* after his first brood there had fledged.

But even if both partners had been controlled each at their first and replacement broods the judgment is not always certain. An example from the study area of the authors may illustrate that: When catching at first broods a ♀ was found standing upright besides the somehow dispersed cold eggs. Though this situation vigorous implicates that this brood was fatal, a ♂ appeared the following night and was ringed. These two birds immediately after began a "replacement" brood in a box 1,4 km apart. The first egg of this brood was laid only three days after the catching action described.

If the feeding (?) ♂ was the father of the first brood we should ask, why this brood had been deserted. There was no evidence of any disturbance. Finally the ♀ (?) still was at the breeding site and her (?) ♂ fed her there. In contrast it could be possible that the father of the first brood had disappeared and the ♂ appearing (for feeding?) was not the father of this brood but a wooer for a widow. This wooer had occupied his own breeding site in the neighbouring village and animated the ♀ to move. In that case indeed the wooing ♂ did not feed his ♀ at the future breeding site. Nothing similar hitherto has been described. On the other hand it is hardly understandable why a ♀ still three days before egg laying should stay at a nesting site different from that of her future brood and then should be fed there and not at the future nesting place by the ♂.

But also another interpretation seems possible which better fits to the biology of barn owls: The ♀ standing aside the eggs had not laid them herself but she was in a box with an abandoned clutch in expectancy of her first egg. The ♂ so fed here his ♀. After having been disturbed by our catching action the ♀ left this box and moved to the new one, which the ♂ probably already before had in reserve as "second offer". The short interval up to laying the first egg supports this interpretation as the most probable one. The new brood thus was no replacement brood for the first one!

This seemingly pedantic persisting in the exact definition of the single second breeding event is necessary for this kind of analyses. It is not so for a more general

interpretation of the situation. The parallel comparison of the success values (eggs/fledglings) between the broods of the first half of the year or those of real first broods on one side and the broods of the second half of the year or the real second broods on the other side has demonstrated, that the relations do not differ substantially. This means, for a general comparison of the success between first and second broods the values of the broods in the two halves of the year even without control of the parent birds give good approaches. So it also does not seem to be aggravating that already the division into the two halves of the year is arbitrary.

After KNIPRATH (2007) in a different population in Lower Saxony the most frequent reason for the change of breeding site from one year to the next for both sexes was the loss of mate. As we demonstrated here, pairs most frequently change breeding site from first to second brood. With a mean interval of 98,3 days between these two broods this change certainly had not been necessary only by the reason that the chicks of the first brood would disturb. At egg laying they mostly had fledged. For this change there is certainly a different reason: In most cases after a brood the nest box has a thick layer of an often humid mixture of pellets, prey carcasses, dung, and probably also parasites. The birds avoid to make a new brood thereon. In our case it was easy to do so on behalf of the high box density. In natural breeding sites such a cess-pool like environment certainly would occur much more exceptionally. Here the chicks spread the dung onto a much wider area in the surrounding of the breeding site itself. So such a site mostly can by used without any problem for a second brood. Perhaps it was the lower number of boxes, which by the reason described prevented a correspondingly high number of second broods in the population around Lachendorf (KNIPRATH 2007). This unhealthy environment may give reason to the lowered longevity of the box grown fledglings compared to that of free-grown ones.

TAYLOR (1994) could demonstrate that the population oscillations in the barn owl directly are controlled by prey availability. The obvious concentration of multiple broods in some few years makes guess that this mechanism also works for multiple breeding. Of course for that it is necessary that barn owls generally breed several times a year, as long as prey abundance does allow. A point in favour of this idea is that in southern Spain, where prey abundance is submitted to obviously lesser oscillations as in central and northern Europe, in nearly all years about 60% of the breeders make a second brood (MARTÍNEZ & LÓPEZ 1999). On the other hand in the study area Altmüller (KNIPRATH 2007) from 1972 to 1992 altogether there were five second broods only (among 152 nest box broods: 3,3%) in qualitatively very different years. Here we should mention that there, in contrast to the area of the present study, there only rarely was more than one box per village. So second broods might have taken place at different not detected places or not at all caused by lack of breeding sites.

In this study the year 1996 is especially predominant (fig. 1): Here the second highest number of broods was registered but only five second broods. It might be supposed that the vole decline already had begun during summer.

In every case each pair has to decide to bread again or not. The cases of divorce second broods described above very evidently indicate that it is the ♀ to make the decision, not the pair. Finally it's her to abandon actively the first brood. Perhaps this interpretation of KNIPRATH & SEELER (2005) is not the total reality: In fact it is the ♀ to desert the first brood in favour of a divorce second brood, but by all means this could

have it's reason in the ♂: In contrast to the ♀ it is not ready for an overlapping second brood with it's raised costs. Accordingly BUNN et al. (1982: 145) describe the procedure: The ♀ takes the initiative and then it is depending on the answer of the ♂ to this initiative whether a second brood will be added. If the reaction of the ♂ is negative, the ♀ following the results of this paper still would have the possibility of a divorce second brood. As a result we may ascertain that each partner makes its own decision.

The results presented made one thing obvious: Barn owls preferably make their second broods with the mate of the first one: 30 out of 56 broods with certain data. But there still is a special strategy for each sex to increase the breeding result of a year without the (still existing!) mate of the first brood: ♂ make a bigyny second brood with a new mate heavily overlapping the first one, ♀ a divorce second brood much less overlapping the first one. Further more there are a few second broods with a new mate, but not overlapping the first ones.

Bigyny second broods
If a ♂ makes a second brood without any participation of the hitherto ♀, it is only depending on the extent of an eventual overlapping (see above) how such a brood should be named. If the broods following each other do not overlap, there is no doubt that the second one is a second brood of the ♂ concerned. (With that we do not ascertain, to which category the brood belongs with respect to the ♀.) If egg laying of the consecutive brood is still within the normal breeding interval (100 days), we, as usual, name these circumstances bigyny. Even if theoretically possible that there is a flowing transition between a heavily overlapping to not overlapping second broods with new ♀, we did not find broods, which only roughly approximated this borderline (from beyond) (see fig. 7). This may be explained by the assumption that ♂ once being occupied with the foraging of heavily growing chicks, no more do charge themselves with the cost of a further, paralleling brood. (In a bigyny second brood with a very early start the amount in time and energy not could have been taxed.)

Anyhow it becomes clear that bigynous relationships (and if they do exist, trigynous ones naturally too) must be interpreted as multiple broods as the ♂ within one year makes more than one brood. The definition "second brood" (see above) is valid also here, even if the brood having been initiated first by the bigynous ♂ later should be unsuccessful. At least at the beginning of the second brood it had been intact. Else the second brood should be defined as replacement brood. The description is facilitated, if the two broods of a bigynous situation are discriminated linguistically: bigyny-first-brood, bigyny-second-brood. Therein the definition as first- or second- is depending on the egg laying. The nomenclature of trigynous situations should be chosen in a similar way.

From these descriptions we may deduce with some certainty that in barn owl ♂ there is no principle difference between monogamy and bigyny: With the beginning of a brood they do have the tendency to establish a further partnership. Indeed they only succeed to do so if the circumstances are very favourable: Only in very good vole years there is the economic basis and only for ♂ of high hunting quality. (In this connection it is astonishing that only about 50% of the double breeding ♂ were experienced breeders. High hunting skills obviously become evident at early age.) Then there must be free and willing ♀ (and for that we should expect a surplus of ♀) and within distance a free breeding site. In reality these conditions only rearly do

coincide. Following the "distribution of resources hypothesis" (ORIANS 1969, cited after GOWATY 1996: 27) this means, the polygony threshold mostly is not reached, most ♂ remain monogamous.

Divorce-second-broods
As already described by ALTMÜLLER (1976), in good years occasionally ♀ desert their still half grown brood (exactly as in very normal overlapping broods of pairs) and make a second brood with a new ♂. In this case the first ♂ alone raises the first brood. Also ROULIN (1998) communicates five cases again in 2002 occupies with the phenomenon under the aspect of brood desertion. EPPLE (1994) named this behaviour serial and GLUTZ VON BLOTZHEIM & BAUER (1994) successive biandry. KNIPRATH u.a. (2004) und KNIPRATH & SEELER (2005), who described more than 20 similar cases, reject the denomination biandry as the ♀ at no instant is engaged in two broods. (Therefore biandry is not included into this study. [Theoretically we could at least count simultaneous biandry as ½ brood for the ♂ and so include it into the frame discussed here.]) Supporting on MILNE & MILNE (1978), GOULD & GOULD (1989) und BAEYENS (1981) they prefer the term (inner seasonal) successive monogamy. As a simple English denomination for such broods there (KNIPRATH u.a. 2004) is proposed: divorce second brood.

The participation of the ♀ in feeding older chicks seems to be very different (BUNN, WARBURTON & WILSON 1982). In the broods studied by EPPLE (1985) the ♀ in all cases shared less and reduced its part even more towards the end of the brood. EPPLE doesn't mention that this reduction of participation only did occur at very good prey abundance what could be supposed in captive broods. If indeed in normal years the ♀ can reduce its participation without endangering the brood, in years with high prey abundance it may assumed that it is of low risk for the first brood if she retires totally for a divorce second brood.

It seems to be a merely academic question up to which temporal overlap of the two broods of a ♀ the term divorce second brood should be used. In the data presented here all eight second broods following up to an interval of 100 days (see fig. 6) were preceded by divorce. Perhaps in the further ones in which the fate of the ♂ is unknown there were some more ones.

It seemed certain that in the divorce second broods nearly exclusively those ♂ "came into action" which in that year not yet had bred (ROULIN 2002, KNIPRATH & SEELER 2005). Thus the surplus of ♂ which must be demanded theoretically for the initiation of divorce second broods is made plausible.

Third broods
Using the above definition of a third brood, the present study could prove none. In the two third broods of two pairs communicated by SCHÖNFELD et al. (1977: 334) details are not clear ("wobei nur zwei Bruten flügge wurden" Wherein only two broods fledged). MULLER (1991) mentions one third brood (out of 1172 broods at all) without entering into the circumstances (like overlapping). Even in captivity FREY (cited in EPPLE 1985:55) could only register third broods "only if first and second broods overlapped, where overlapping of the clutches was facilitated and reached by offering two boxes".

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Comparison of the second brood strategies
No doubt, depending on the short lifetime in the result for a barn owl it is much more advantageous to make a second brood than to wait for further year. Comparing the second brood strategies then illustrated that assessing is different for the ♂ than for the ♀: These latter ones indeed are still a little more successful when changing their mate for a second brood than when staying with the former one. Nevertheless they rarely use this option. For ♂ however at any case it is evidently more successful to stay with the previous partner and to make a second brood with her. Yet the "hope for a quick success" (Who really does know, how the situation will be three months later?) makes bigyny attractive for ♂.

Overlapping
Overlapping of two broods generally is possible only for ♂, as they can realize in parallel duties at more than one brood. The ♀ in contrast incubate beginning with the first egg an so cannot share in feeding the previous brood. This is identical for second broods of pairs and for second broods with new mate. If a ♀ is willing to make a second brood with shortened interval, so this always means that she stops her participation in her previous brood.

Overlapping broods for the always mean a double burden, indifferent whether it a with the ♀ of the first brood or with a further one. He has to feed both ♀ and the young of his first brood and in addition to provide the nutrients for the production of the second clutch. If the two broods overlap only at a minor degree at least it is not necessary to furnish two groups of siblings in parallel. In bigynous broods this indeed is the case. Thus these in fact are especially loading and therefore only do occur in really exceptional years and have the lowest overall success of all second brood strategies.

EPPLE (1985:81) in detail discusses the burden of the ♂. Additionally he pleads for a considering of all second broods as overlapping because occasionally ♂ still feed their young at an age of 115 days (observation EPPLE 1985:81).

Already the handbook (GLUTZ VON BLOTZHEIM & BAUER 1994:255) points out that some of the broods in the (German) literature called "Schachtelbruten" (overlapping broods) more likely were cases of bigyny not recognized. (Parent birds had not been controlled at both broods.) Following the numbers of the present study (15 overlapping broods of pairs versus 10 cases of bigyny) we could agree in 2 of 5 cases.

5. Summary
For the present study a nest box population in the eastern forelands of the Harz mountains (9.87E, 51.82N) has been studied from 1996 to 2006. The total of boxes oscillated around 300 with a density of about three per village (N=99). The evaluation is based on 435 broods. 82,2% (♂: 79,5%, ♀: 86,0%) of the breeders were controlled and all chicks ringed. To test differences we used ANOVA as integrated in MS EXCEL.

Like the total number of broods the number of second broods (third broods were not found) oscillated widely between the years (fig. 1). Only 4 of these 11 years were such of higher numbers of second broods (1998, 2001, 2004, 2005). We fond 74 second broods, i.e. 21,3% of the yearly first broods were followed by second broods. The numbers of second broods of a year was closely connected to the year to year alteration of the total brood numbers.

In total 421 (228♀, 193♂) breeders were controlled, only 87 of which (20,7%) were engaged in second broods at all. One ♂ participated in three, two in two each and the resting 33 in only one. For the ♀ the numbers are: 2:3; 5:2; 41:1.

The average of fledglings significantly differed between first and second broods: The second broods had the minor success (5,3 respectively 3,8; P<0,001).

In the second broods we found different categories: In 30 (=40,5%) of these the breeding pair made the second brood in common. Further 13 ♂ and 13 ♀ (together 35,1 % of the second broods) made a second brood but with a new mate.

The time intervals between the two broods of the pairs differed between 69 and 113 days, on average 92. These differences seemingly were not dependant on egg laying of the first brood.

As the strategies of the sexes could have been different we studied their second broods separately. Mates and egg laying data for both broods are known for 13 of the 23 double breeding ♀. They overlapped similarly to those of the double breeding pairs. Up to an interval of 100 days that means: In favour of their second broods all these ♀ had deserted their first broods and their first mates as well. All these deserted broods (N=8) were successful (mean fledglings 6,3), the following second broods of the respective ♀ indeed much less (mean 4,8)(ns).

As in the double breeding pairs and also in the ♀ with a new ♂ some of the second broods of the ♂ with a new ♀ overlapped, others did not. Different to the former two categories the intervals in the latter one the lower intervals were much lower (15 days twice versus 69 days). These considerably overlapping broods commonly are called bigyny. The 10 cases of bigyny exclusively were fond in the four years with the highest numbers of second broods. These years were those with most distinctly increasing brood numbers. Two each of these first and second broods were unsuccessful. Measured as well by clutch size (mean 6,3 und 6,4) as by the number of fledglings (3,7 each), the ♂ invested equally much into both of their broods. Nevertheless they were much less successful than those ♂ which performed their second broods with the mates of their first ones (mean fledglings: 10,2; P<0,01). Comparing egg laying of single breeders to that of the first broods of double breeders we found a mean of day 103,5 in the former, and 105,1 in the latter ones (ns). The mean of fledgling even was identical (5,48). Thus double breeders invest as much into their first broods as single breeders do into their single ones. We suggest that their could exist two different life strategies: (1) to breed with all effort as long as circumstances are favourable or (2) to save power fore a further career as breeder. For this second option a favourable survival rate is essential. Surprisingly the double breeders reached the following breeding season at a far higher probability than single breeding individuals (23,5% versus 13,2%). To make a second brood or not is not a question of strategy. Following the data presented this evidently is not an alternative. In fact it looks much more as if in both sexes this was a question of quality. The individuals of higher quality preferably make a second brood and even more they also live longer. This idea is supported by the fact that there were three ♂ and five ♀ which during several years were engaged in two or three second brood events.

The mean values of the intervals of all strategies differ significantly with the exception of those between the second broods of pairs and those of ♀ with a new ♂. In the

latter ones the second broods follow the first ones after 91,7 and 92,8 days. The intervals of second broods of ♂ with new mates are much shorter: 48,0 days. These broods in majority belong to the category bigyny. If the latter ones (N=9) are separated from the true second broods (N=3), these latter ones do have an interval of 105 days, the other ones of 29 days.

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