

Divorce and pair fidelity in the Barn Owl *Tyto alba*

By Ernst Kniprath

1 Introduction

Following Davies (1992, cited in Ens et al. 1996: 345) pairing systems generally should be looked at as “outcomes of the decisions made by individuals, each selected to maximize its own success“. This of course is as well true for that part of decisions, which lead to the maintenance or to the solution of a pair bond.

To recognize divorce as such presupposes that in a not too small population over a longer time period a maximum of individuals is identified in the context with their broods. For barn owls, which are active only during darkness, colour-marking is hardly applicable. So besides observing single broods or using telemetry only capture and ringing remain. Barn owls as very willing nest-box users offer good suppositions for this method. So there do exist several papers for this species, in which qualitative and quantitative results are presented on divorce, three on divorce during the breeding season (Altmüller 1976, Roulin 2002, Kniprath & Seeler 2005) and two on such from one season to the next (Kniprath 2007, Kniprath & Stier 2008) and two more on special fidelity and specially divorce frequency (Kniprath & Stier 2005, Seeler & Kniprath 2005). The data to all these papers originate from nest box populations.

Here we shall try to depict, which information concerning the subject divorce is contained in the data of broods and controls of a local barn owl population and how to interpret them. Divorces probably are not sudden events. They might be preceded by actions of the mates concerned, which already no more might be consistent with absolute (what only can mean: genetic) mate fidelity. Actions of that kind also can be episodes, which finally do not lead to divorce. The actual data also will be studied in this connection.

Material and methods

The data were collected from 1996 to 2009 in the northern part of the district Northeim in southern Lower Saxony/Germany (ca. 520 km²). All broods (520, including those, which already were “deserted” when we found them) took place in nest boxes. All chicks and a maximum of the parent birds were ringed. For 395 (76,1%) of these broods both parents are known, for 66 (12,7%) more one parent (51 ♀, 13 ♂). Altogether for all broods thus a proportion of 82,3% (78,6% for the ♂ and 85,9% for the ♀) of the parents is known. Here we count bigynic relations as two pairs.

During the study period the number of nest boxes in the entire study area was greater than two for each village. So the owls at any time could move within their village. The boxes, which had been used by the owls, were cleaned every year during winter time.

In the literature we find as a basis for the estimation of the proportion of divorce the “pair-years” (= number of consecutive year-pairs the pair-partners are living; Black 1996: 14). This definition, basing on species, which breed only once per year, ignores the additional broods of multiple-breeders within a single breeding period. As barn owls indeed repeatedly make more than one brood per year (see Kniprath & Stier 2008), the classification into “mate fidelity” or “divorce” that way is not possible clearly. It may

happen that ♀ after a divorce-second-brood (with a different ♂; for definition see Kniprath et al. 2004) perform their first brood in the following year again with their first mate. Following the definition of pair years this pair is faithful. At least the ♀ was not so at all (neither to the first nor to the second ♂!).

From every brood to the next one within a breeding season a pair might be faithful or not. And again from the last brood of a season to the first brood of the next season a pair may stay together or not. Here a definition of the kind “pair-cycles” (= number of consecutive brood-pairs the partners are living) is better as multiple broods can be included. In the following this definition will be used. We will also count as proven pair-cycle if the survival of both pair-mates to the following cycle only was deduced from the controls of later years. Here indeed it is necessary that for at least for one of the two partners a brood with a different mate has been documented.

For simplicity reasons we will follow Black (1966a) and use the more comprehensible terms “marriage” (instead of “pair formation”), “divorce” (instead of “rupture of the pair bond”), and “fidelity” (instead of “maintainance of the pair bond”). They only serve description and don't contain anything of the juridical, religious, and ethic contents in the domain of human associations.

3 Results

3.1 All pair-cycles

266 of the 395 pairs with both mates know only once were documented, 74 more made two broods together, 11: 3; 3: 4, and 2: 5. These common broods not always followed each other uninterruptedly. So from these numbers neither the other values used below nor the entity of pair cycles may be derived directly.

Altogether there were 91 pair-cycles. For 71 (78,0%) of them the partners remained faithful, 20 (22%) separated. The case of a “faithful” pair from year A to year B, in which the ♀ in year A had a second brood with a new ♂ but divorced and returned to the first one for year B (as mentioned above), is not included into these 71 cases of pair fidelity.

The 91 pair cycles spread over nearly all years of the study. Figure 1 associates them to the year of the start of the respective cycle.

Figure 1 shows the alterations in the numbers of broods and the pair cycles found during the years of the study, figure 2 that there were divorces only within, respectively after only eight of altogether 14 years. No connection with the all over number of broods in the respective year is recognizable. Nevertheless the number of divorces was the greater the more the numbers of broods had augmented compared to the preceding year (fig. 3). This indeed is not true for the relative numbers of divorces in the single years. There is no correlation (no fig.). The supposition, among the divorces in the two extraordinary good years there preferably were the divorce-second-broods did not verify. Without these the diagram did not alter compared to figure 2.

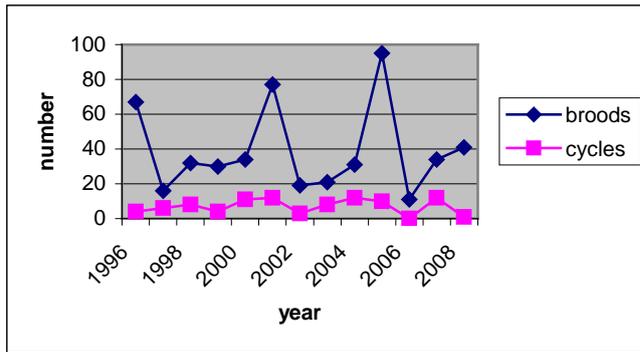


Figure 1: The total numbers of broods in the study area (n=508) and the pair-cycles found (n=91) during the years

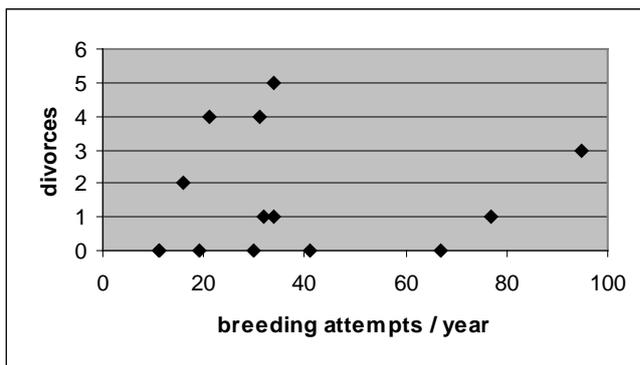


Figure 2: The number of divorces in relation to the number of broods in the same year (n=21)

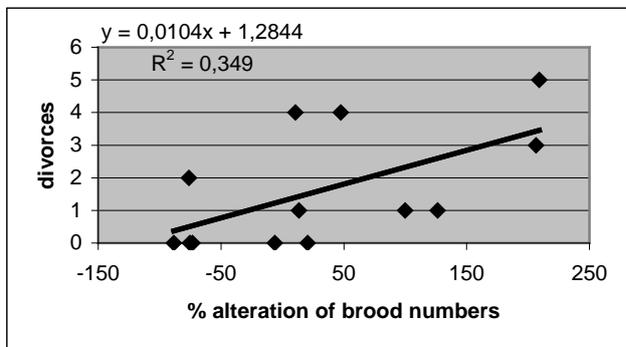


Figure 3: Number of divorces of a year in relation to the proportional alteration of the brood numbers compared to the preceding year (n=21)

Six of the 71 faithful pairs (8,45%) were not successful at their first brood whilst three of the 20 pairs with divorce (15,0%). The mean breeding success counted as fledglings was 5,6 and 4,85 resp. (ANOVA EXCEL: ns). With respect to the success of the consecutive broods within a cycle the faithful pairs (mean fledglings 4,8), the divorced ♂ (4,85), and the divorced ♀ (4,5) only negligibly differed in their success (ANOVA: ns). Comparing first and consecutive broods of faithful pairs (5,6 and 4,8) gave a P=0,059. For the divorced pairs the success of the consecutive brood (4,6) compared to that of the preceding one (5,1) was slightly smaller but insignificant as well (P=0,5). Insofar there was no difference between the sexes.

The faithful pairs stayed in their box (38,2%) or moved within the village (<500 m) (55,9%). At least 5,9% moved to the neighbouring village. (The two maxima 2,6 and 5,3 km belonged to replacement broods.) As moving distances we found for the divorced birds (tab. 1). Testing the original distance values by ANOVA showed with a P at 0,01 that ♂ and ♀ move for significantly different distances after divorce.

Table 1: Some values concerning moving distances (km) after divorce

	N	MW	Median	Max
♂	20	1,1	0,27	6,3
♀	21	3,38	2,1	13,7

Besides the already analysed aspects of divorce with respect to pair-cycles there is still the “personal” level. 32 of the ♀ were faithful only once and 30 of the ♂; one ♀ six times each and two ♂ four times each (fig. 4). The numbers concerning divorces were similarly close together (fig. 5).

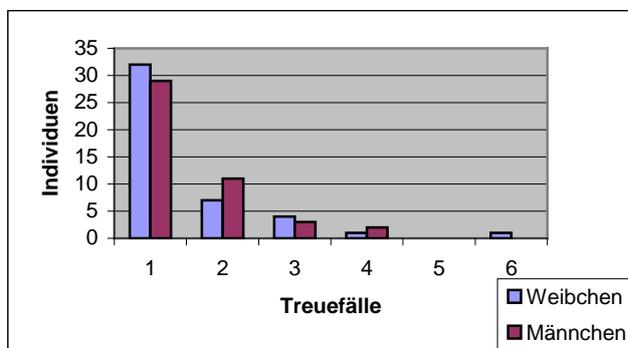


Figure 4: The cases of fidelity of the shared individuals

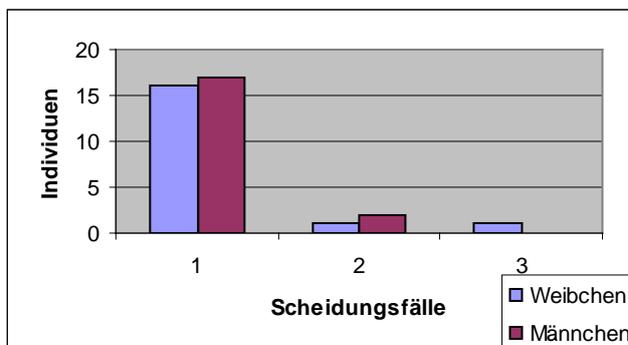


Figure 5: The cases of divorce of the shared individuals

This summarizing could provoke the impression that divorce and mate fidelity would mutually exclude in the individuals involved, would be something like an attribute. That indeed is not generally so. There were a ♀ with two pair-cycles, one of these faithful and the other one with divorce; one more with three cycles, once faithful, twice divorce. For one ♂ we found five pair-cycles, thereof two with divorce and three with pair-fidelity.

Age of mates

Partly the exact age of the breeders is known for they were ringed as nestlings. In this study the unknown immigrants were included as well. They here all are estimated being yearlings. For the figures the age-stages were comprised to groups (figs. 6,7). As to the frequency of divorce there is a difference between the sexes: In the ♂ (fig. 6) the

divorce rate in the middle aged birds is obviously smaller than in the two other groups, in the ♀ in the present material there is no such difference (fig. 7).

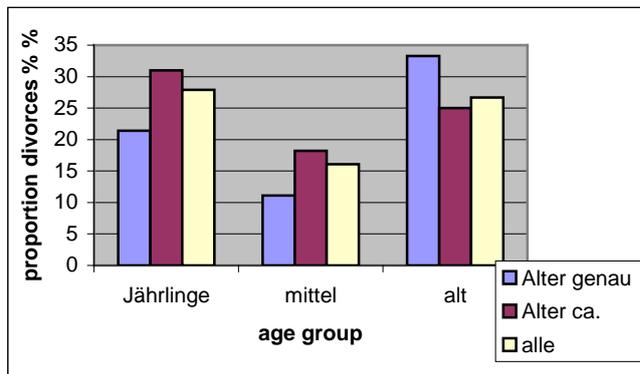


Figure 6: Divorce rates of the ♂ per age group (middle: 2-3 years, old: >3 years). (yearlings N=12, middle=5, old=4)

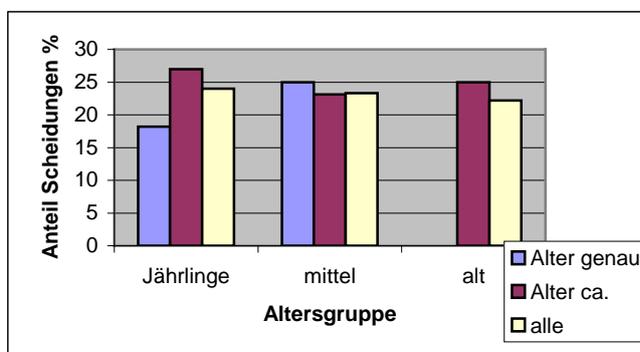


Figure 7: Divorce rates of the ♀ per age group (middle: 2-3 years, old: >3 years). (yearlings N=12, middle=7, old=2)

3.2 The different pair-cycles

We followed the supposition, the different types of pair-cycles could show differences when studied separately.

a) Pair-cycles without second brood / replacement brood intercalated

Both partners of 27 pairs, which in their first year have had neither second nor replacement broods survived to the following year. Out of these 22 (81,5%) were faithful, 5 (18,5%) divorced. The faithful pairs stayed in the same box (72,7%) or only moved within the same village (22,7%). At least 4,5% for their consecutive brood moved to the next village. Among the divorced owls none of the two partners stayed at their common breeding site. Thereby the ♀ moved farther (mean 4,1 km; median 3,8 km) than the ♂ (mean 1,8 km, median 2,1 km) (ANOVA. ns).

Comparing the means of first broods (4,9 fledglings) and successive broods (4,5) gave no significance (ANOVA) for faithful pairs. After divorce this value mounted from 4,8 to 5,0 for the ♂. For the ♀ it fell from 4,8 down to 4,0. These differences too are not significant.

b) Pair-cycles of first and second / replacement broods

From a first brood in a year to a further breeding event within the same year there were 52 pair-cycles. Among these for 37 (71,2%) the mates were faithful (34 second, 3

replacement broods), for 15 cycles (28,8%) the partners divorced. The faithful pairs stayed in the same box (10,8%) or moved inside the village (81,1%). At least 8,1% moved to the neighbouring village for the consecutive brood. Here the two maximum values of 2,6 and 5,3 km were those of replacement broods.

In the cases of divorce seven times the ♂, never the ♀, and eight times none of both stayed in the box of the first brood. Here the differentiation is a little more complicated: Ten of these events (66,7%) were divorce-second-broods of ♀ (where the ♀ deserted their first broods distinctly before their young had been independent, and the respective ♂ alone reared the first brood (for details see KNIPRATH & STIER 2008). None of these ♂ later had a second brood. Indeed 77,8% of them again were mated the following year, if they did survive at all (N=9). The remaining five divorced ♂ for which the distance between the two broods was as long that can be assumed the two partners had finished this first brood and only then divorced. The five ♂ subsequently made their own second brood with a new mate. Onto the 10 ♀ with divorce-second-brood there were five with divorce after the first brood. Three of these made a second brood with a new ♂, two a replacement brood (for the unsuccessful first brood). That means, all ♀ which abandoned their mate within a breeding season, subsequently made a new brood (breeding effort). So for a comparison of the moving distances there are four groups: ♀ to divorce-second-broods (n=10; mean 4,0 km), ♀ to normal second broods (n=3; 0,6 km), ♀ to replacement broods (n=2; 0,8 km), and ♂ to second broods (n=5; 0,2 km). It is striking that the ♀ moved the multiple of the distances of the other categories. As could be expected (numbers too small) these differences are not significant (ANOVA).

Table 2: Comparison of the success values of faithful and divorced barn owls between first and second broods (by sexes) (divsecbro = divorce-second-broods)

		mean young fledged		P
		brood 1	brood 2	
year1 - year2	faithful	4,9	4,5	0,50
	M divorced	4,8	5,0	0,90
	W divorced	4,8	4,0	0,70
first-second	faithful	6,1	4,8	0,01
	M divorced	6,5	5,0	0,30
	W divorced	5,3	3,3	0,55
	W divsecbro	6,5	5,4	0,30

Comparing of the success values of broods before and after divorce demonstrates that the brood together with a new mate nearly always was worse (all ns). The first exception are the ♂ from one year to the next. They gained (ns). The other ones are the pairs faithful from the first to the second brood. This latter one for them was significantly worse.

c) Pair-cycles as combination of second, third or replacement broods

In the study area no third brood hitherto has been observed. So there is no cycle with a third brood. A brood following a replacement brood as well as a replacement brood after an unsuccessful second brood did not occur. Indeed all these combination generally are possible.

d) Pair-cycles of second / replacement broods and first brood of the successive year

We found ten cases in which the pair partners of a second event of a year again were controlled during the breeding season of the following year. Nine of these pairs remained together until to the next brood, one pair divorced (after a replacement brood). For five of the faithful pairs the preceding brood had been a regular second brood. In two of the basic broods each of the ♂ had a second brood, a bigyny-brood. They both remained faithful to the ♀ with the later laying date. These two later ones and also one of the earlier bigyny-broods all were successful. For the two remaining pairs the basic brood belonged to different brood categories.

Seven of these pairs stayed in the same box or (3) moved within the village. None of the partners of the divorced pair stayed in the box of the first brood.

We still have to examine whether the original values of the moving distances of the different cycle types do differ (ANOVA). When all the values of the cycle types a), b), and d) named above were tested in common there was no significance ($P > 0,1$). If the three values for replacement broods integrated in b) were introduced as a separate group into the test we found $P < 0,001$. After excluding these three values from the test, the P again was $> 0,1$. So the statistic treatment showed that only the moving distances of faithful pairs to replacement broods differed significantly from all others. Nevertheless the summarized moving values contain something biologically interesting: Second and replacement broods almost never took place in the boxes of the first brood. For their consecutive brood in the following breeding season the faithful pairs in $> 70\%$ of the cases used the same nest box.

3.3 New mating

Barn owls might again become unmarried not only by divorce but also by the death of their mate. Of the known 854 owls (408 ♂, 446 ♀) 179 (108 ♂, 71 ♀) suffered that fate as recorded (as they survived and were controlled again). Up to the following breeding season 86% (83,3% ♂, 90,1% ♀) were paired again, for 12% (14,8% ♂, 8,5% ♀) of them it took two years until they were controlled again as breeders. The small rest for which it took longer is neglected here. It is of interest whether divorced owls remain longer unpaired than widowed ones. For these latter ones the numbers are: in the consecutive year 85,7% (77,8 ♂, 100% ♀), one more year later 14,3% (22,2% ♂, 0% ♀).

Remating

When looking for the reasons of divorce, the phenomenon remating (of mates which already had been a pair) could be helpful. All together five times the former divorced pair again came together. All these owls had found a new mate after their divorce, four of them immediately after. Two of these remated ♂ and four of the ♀ again had divorced in favour of this remarriage.

3.4 Non-breeders controlled during the breeding season and over winter

We had 155 controls of non-breeding owls. These were dispersed as well among breeding seasons as among winter months. Almost 135 owls were concerned. 41 of these were controlled neither before nor after. Of the remaining 94 ones 56 were controlled repeatedly (> 2 -fold) but only 12 also between two of their broods. Only for one of these cases we have enough concerning data: Linde (names facilitate recognition here) separated from Kai for a divorce-second-brood with Neander. In the following she stayed with Neander. The following springtime Kai was found together

with Otilie in “his” box. Nevertheless he later bred there with Olivia. Still that season Olivia bred with Oskar some kilometres apart. This obviously was a trial of Kai to have a new partnership with Otilie after his divorce from Linde. Because Otilie moved and Kai stayed it seems evident that it was Otilie to finish this attempt. Thereafter both, Kai and Otilie, were successful in finding a new partner.

4 Discussion

When judging the certainty of the numbers presented here it is important to know that never all breeders but always only a portion of about 80% was controlled. So there could have been as well 20% more pair-cycles than really detected. Generally this is true likewise for the frequency of pair fidelity and of divorce. However to prove fidelity only the repeated catch of two owls is necessary, to prove divorce we need that of at least three (the original pair and an additional new mate). The probabilities of evidence thus relate like 0,62: 0,5 in favour of pair fidelity. This relation indeed may still be a little worse basing on dismigration at the borders of the study area. The ♀ generally move farther than the ♂ and especially farther than faithful pairs.

Numbers of pair cycles in the barn owl hitherto only once have been published (Kniprath 2007). For 151 broods registered at all in the study area Lachendorf (about 220 km²) 18 pair years had been found. Among these there was only one divorce (5,6%). Additionally among the five second broods there were two of the original pair and two divorce-second-broods. Following the definition used here there were found 23 pair-cycles with three divorces (13,0%). There the relation to the all over number of broods was 15,2 facing 17,1 here. The proportion of breeders controlled there was mostly identical to the numbers communicated here (77,0% ♂, 83,1% ♀). The difference in the relation consequently more likely may not be explained by different controlling intensities. This also holds true for the astonishingly small proportion of divorces (13,0% against 23,6% here). Probably there is a correlation between the extent of the study area (220 km² Lachendorf; 520 here) and the known number of pair-cycles and the proportion of divorces as well. All these numbers are smaller for the smaller area.

It shows to be a very basic lack that of course only those divorced owls could be identified which had found a new mate and bred. So by methodical reasons we cannot make any statement whether for divorced owls there might arise costs for not finding a new partner and for not breeding again. We found indeed that divorced owls afterwards were again found as breeders with about the same frequency as widowed ones. The proportion of nearly 20% in both groups for which we succeeded to find a new breeding only later, more likely is attributed to the fact that on average we did not succeed to control breeders in a similar magnitude.

On one hand we did not find any correlation between the all over numbers of broods and the numbers of divorces of a year and on the other one a positive one with the increase of the broods compared to the preceding year. That leads to the supposition that divorces predominantly happen when the rodent numbers rise before and during the breeding season.

Divorce and the background

With the calculated divorce proportion of 22,0% of the pair-cycles the barn owl had a divorce rate of about twice that (11,3%: Newton & Wyllie 1996: 256) of the sparrow

hawk (*Accipiter nisus*) being generally resident, in part continuously and in part part-time paired. This bird has a similar size and a nearly identical duty sharing between the sexes concerning brood and elevation of their descendants (Newton & Wyllie 1996). Numbers for other European owl species obviously do not exist.

In relevant hand-books (Niethammer 1938, Glutz & Bauer 1994) and monographs (Mebs & Scherzinger 2008) the barn owl at least for Europe is said to be “faithful to its breeding site”. Indeed it is of importance for the interpretation of the fidelity situation to know, where these site-faithful barn owls in fact live outside the breeding season. If both partners stay in their home ranges than they keep in connection and the pair bond may persist (permanent partnership; for definition see Ens et al. 1996). In this case divorce means that at least one partner must become active.

If indeed at least one partner leaves the home range for a longer period (weeks or months) and then comes back again this means part-time partnership. Here the partners (or a third bird) may play fairly different roles. So first we had to clarify, where the “resident” owls in fact live outside the breeding period. Telemetric studies at least up to the autumn (Brandt 1992, 1995) had shown that the adult owls may extend their home ranges, sometimes also may shift them. The analysis of the data of a population in Lower Saxony mostly controlled by R. Altmüller had shown that also adult barn owls may move between two breeding periods (Kniprath 2007). These owls nearly exclusively were ♀ and additionally those which had lost their partners.

Multiple records by which perhaps conclusions could be made first have been analysed by U. Sauter (1956). The recovery data of the Vogelwarte Helgoland, which had been augmented essentially since, lead some steps farther (Kniprath & Stier-Kniprath 2009). It was found that between the breeding periods certain but mostly insignificant locomotion may happen. On one hand wandering was found between breeding period and winter time and on the other hand between winter time and breeding period. Also here there was no proof for any movement to and back again. Altogether it seems clear that barn owls, which once have settled, also during wintertime stay at their home range or in proximate vicinity to it. We may derive that barn owls (may) keep contact outside the breeding season and thus (may) live in permanent partnership.

For barn owls there are very different time intervals between one to two or even three possible broods in a single year and/or up to the consecutive breeding period. Sometimes between first and second brood there is an overlapping, i.e. no distance. In contrast, intervals up to 15 days (=interval between the two egg laying dates – 100 days for the normal brood duration) may occur (Kniprath & Stier 2008). As for replacement broods we never know the date of the end of the first brood the distance between the latter date and the start of the replacement brood cannot be ascertained.

Compared to the very short intervals between first and second / replacement broods those between the broods of two consecutive years – even between a late second and an early first one – are very long. It is always the question of months. The very important difference is that in the latter cases the sexual activity probably goes down for a longer period. The conditions for maintaining the pair bond thus are very different. Counting 28,8% the divorce rate from first to second / replacement broods is considerably higher than that from year to year (18,5% after a single brood respectively 10% from a second brood to the brood in the following year). May the lower hormone

level make more tolerant against negative experience in the pair bond or are there other reasons?

As a possible reason for divorce unsuccessfulness is discussed (Black 1996a, Ens et al. 1996). The data of this study give no useful indications that this reason might exist. The pairs which divorced later had a higher proportion in totally failed broods (15,0% against 8,45%) but in their successful broods the result was better (5,6 young against 4,85). Comparing first broods to the consecutive ones in two of the cycle-types (*a* and *b*; only for these there were sufficient data) shows (table 2) that the consecutive broods nearly always had a lesser result. This agrees with the results of earlier authors dealing with different species (for list of authors see Black 1996a: 13). But as faithful pairs in this comparison as well always had an inferior result there still must be (also) additional reasons.

It seems astonishing that ♂ gain after divorce from one year to the next. This could be an indication that in this type of divorce problems of compatibility could have been the cause. This supposition of course collides with the result that in divorce ♀ mostly are more active (see below).

The divorces of ♀ for divorce-second-broods certainly not are attempts to find a ♂ of higher quality (Kniprath & Seeler 2005) and thus to increase the personal biological fitness. At least the first brood totally is surrendered to the first ♂ for all further elevation. Nevertheless this divorce means an increase in fitness for the ♀ as so a consecutive brood may begin earlier and in addition takes place in a territory in which the own young of the first brood not must be furnished as well (W. Scherzinger per E-mail)

Who initiates divorce?

There is no doubt concerning divorce-second-broods that the activity exclusively comes from the ♀ for it is her to move and so to desert the ♂ together with the first brood. All other "normally" divorced owls sometimes within the same year but mostly in the following year added another brood. From there we cannot derive anything about who was the more active part. Also the divorced ♀ in their successive broods not were more successful (mean 4,6 young) than the divorced ♂ (4,6), and as well as faithful pairs (4,8). There are probably other reasons for the fact that the success of new broods generally was inferior to that of the first ones. Hereto we count the general quality of the respective years and also whether the subsequent broods had been second broods or first broods in the following years. However, the data are insufficient for discrimination.

Direct observations, which could give an exact indication, probably do not exist. Nevertheless we find evidence in the behaviour of the owls following divorce. In fact, moving after divorce presupposes activity. If after divorce one of the partners at all stayed in the box then it were the ♂ (7 cases among 15 divorces). That too implicates more activity of the ♀. All divorced ♀ moved, yet additionally in eight of the 21 cases the ♂ as well. As the ♂ generally are the more philopatric sex (Kniprath 2007), we certainly should assume weighty reasons. So we assume that indeed they too actively participate in the divorce, probably sometimes are the more active sex.

Barn owls moving after divorce obviously make every effort to find a new possibility for breeding as close as possible. Herein the ♀ are more successful than the ♂ (see table 1). When regarding only divorces from a first brood to a further breeding event during

the same year we see immediately that the distances to replacement broods are fairly larger, even for faithful pairs. The loss of a brood seems to have a traumatic effect. This could cause a farther moving. Likewise those ♀ moved farther which abandoned their previous ♂ for a divorce-second-brood. This probably was not an "intention" but the sequence of the situation. At the moment of the desertion the other broods all were going on. That means, the choice in nesting sites was scarce and especially that in unmarried ♂. (This likewise is true for the cases of bigyny. The distances of the respective broods from each other are distinctly greater than those of second broods (Kniprath & Stier 2008).) The situation had changed for those who executed divorce only after finishing their first brood: Then free boxes and candidates for mating were available at nearer distances.

Age

When calculating the portions of the age groups in the divorces, all immigrants were counted as yearlings. This method indeed sometimes underestimates their real age. Sometimes one of the immigrants was not controlled during his first year of presence. Likewise it may be (as demonstrated for marked birds) that an owl immigrates, which no more is a yearling. So the respective columns in the figures 6 and 7 are rather to high and those of the group "old" to low. But as the relations between the numbers of the age groups are mostly identical, this fault might be neglected.

The partition into three age-groups (yearlings, 2-3 years old, and >3 years old) seemed to fit best to the low longevity of most barn owls. Yet in this partition the group "old" encloses only a few values.

The differences in divorce frequency of the sexes between the age groups as appearing in the figures 6 and 7 must be doubted because of the low numbers (for both sexes 21). Nevertheless it doesn't seem altogether as if there was a higher proportion of divorces in the yearlings as had been described for other bird species by different authors (Ens et al. 1996: 353). So we estimate that the reduction of the divorce portion with age as formulated by Ens et al. (loc. cit.) as prediction1 is not suitable for the population studied.

If the first brood of a pair-cycle had been a second brood, the faithful pairs (and the divorced ♂ as well) more often stayed in the same box for the succeeding brood in the following year than if it had been the transition from the first brood in a year to a further one in the same year. This difference certainly has no significance but a ecologic cause: Barn owl boxes after a brood very often contain a thick layer of pellets, faeces, and prey remnants. The owls preferably avoid to start a further brood on that. As in close vicinity nearly everywhere there were sufficiently free boxes they had no problem. Yet they had to move. After our usual box-cleaning during autumn the same boxes could be used for a further brood.

Events in the transition between mate fidelity and divorce

In barn owls genetic monogamy in pair bonds is the rule but there are rare exceptions (among 54 broods in one, among 211 young a single one: Roulin et al. 2004). Already here we see that the image of mate fidelity and divorce is not black and white. Here the occasional cases of bigyny (for details see Kniprath & Stier 2008) must be mentioned, which, though they are not connected with divorce, certainly do not fall into the category mate fidelity.

The results of divorce

As already discussed above, in this study divorce only was detected if both partners were controlled later on and if at least one of them bred with a new mate. There is no record of a divorced owl, which later lived in the study area without a mate. For those divorced owls, for which a new breeding record could be furnished only later, we mostly suspected that they were present but not controlled. The further discourses must be seen under this reservation.

Divorced owls found a new mate as quickly as widowed ones. Also the values of success before and after divorce resp. loss of the mate do not differ in both groups.

The astonishing high portion (5 of 21) with which divorced owls again found together makes guess two things: On one hand the cause of the divorce might not have been in the persons of the mates. On the other hand indeed learning by a bad experience and the return to the “minor evil” can be imagined. We are confirmed in this interpretation in so far as two of the ♂ and four of the ♀ separated from the “interim mate” for this new marriage.

4.1 The background of divorce

The subject divorce – as interesting it is per se – probably will be better understandable if we see it as part of a general, permanent life-decision: Should I stay where I am right now or should I better be elsewhere? The decision situations of the owls shall be depicted as a model.

The decision situation

Living beings make demands on their surroundings. They compare the realities they realize around them with these demands and then decide: stay or not. As permanent fields of demand we can imagine: safety (roosts, predators), food (prey, competitors), and seasonal ones: breeding sites and partners. The concrete demands on one hand certainly are given endogenously, on the other hand are adopted by experience during their time as nestlings and up to their independence. In their extent they are altered during their childhood (behaviour of parents and siblings), body mass, constitution, hormone level, and the depending self-assessment. Steady experience acts as a corrective.

The factors acting up to and in the concrete decision situation are summarized as a model in figure 8. The realized reality of each demand thought, in a very differing extent fits to the individual “level of demand”. The sum of the deviations gives the “level of fulfilment”. Depicted in the figure as well is the “level of emigration” meaning the level of fulfilment beyond which the bird decides to emigrate. At each level of fulfilment above that and especially if the level of demand is exceeded, at first there is no reason to move: The owl stays at the present site. Yet the owl may emigrate if it believes to recognize from its home range that in the surroundings its demands might be fulfilled still better.

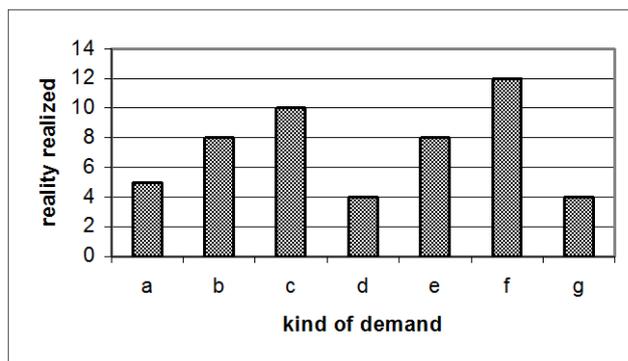


Figure 8: Model of the demands of an individual, their levels realized, of the own averaged level of demand (- - -), of the subjective level of fulfilment (.....), and of the level of emigration (----) (see text) [The fig. only is complete when using layout-mode]

By different individuals the various demands presumably are weighted differently. That may implicate that a single demand (safety, food) alone lowers the level of fulfilment in an extent that it sinks beyond the level of emigration. The owl will emigrate unconcerned how good the other realized realities fulfil other demands. Vice versa we may imagine that a single demand, which is over-fulfilled, can darken the sight on the reality of other demands.

This general situation, which is valid all around the year, during the season of reproduction is superimposed by additional demands (breeding site, mate). So we can expect that ranges, which at all fulfil the general demands but not the brood-specific ones, at least with starting breeding disposition will be abandoned. (That is the background of the observation often communicated: "Until February they were present!") If these new demands are fulfilled without change of range, the owls self-evidently at first stay. Thereafter indeed the behaviour of the sexes will be different.

Following the literature (Epple 1985) the ♂ "occupies" a site and offers it (and himself) by screeches and demonstrative round-flights. Thereby it becomes obvious that for the ♀ the demand for a breeding site is fulfilled. Possible mates in turn test in several steps (Epple 1985), whether site and candidate fulfil their demands as far as visible. They will stay or wander (as above in 3.4 is described for the case of Kai and Otilie). Whether the ♂, which is strongly fixed to the site (Glutz & Bauer 1994), has a chance to reject the applicant or even to move is uncertain.

If then during breeding the original judgement of the site and/or the mate proves as wrong, a new factor superimposes the decision: the investments done hitherto. The longer the brood already lasted, i.e. the more had been invested, the more in the case of requirement the level of demand is lowered. The partnership is not given up immediately. As soon as the realities concerning breeding site and mate lead to the end of the brood, then a decision on the partnership may be actual. If already during the brood the level of fulfilment of the general demands makes worse, the brood will suffer but it is not necessarily reason for a separation of the partners after the brood.

If however the miss-estimation concerned the level of the mutual behaviour of the mates, the brood presumably will suffer as well, but – on account of the investments – will not be abandoned but somehow lead to an end. Then indeed the soon separation of the mates is to be expected.

Of course being originated in the “persons” of the mates but at a different level there is the case of some illness of one of the partners which leads to the temporal failure in caring for the brood. At least if the ♀ fails during the incubation or brooding phase the brood will end. The same is valid for a failure of the ♂ during these phases. It is indeed imaginable that then also the partnership ends for the healthy individual doesn't like to miss that season for reproduction. But it is not necessarily so: In the study area of the author in 1996 at the end of the brooding phase the ♂ for at least three weeks did not participate in providing the brood (unsuccessful trials for catching him). Then he reappeared with a deformed backward toe and a turning toe with a regenerated rupture. During his absence the three youngest pulli disappeared. This failure obviously had not led to the end of the pair bond. Probable he had not been physically absent but only not ready for service.

Onto these reasons for separation founded in the pair partners there are more, which will be depicted in connection.

Schedules

The scheme of the possible proceedings of divorces in Ens et al. (1996: 349) (fig. 9) contains three variants: (a) abandon (of the hitherto partner), (b) chasing (of one partner by a third individual of the same sex), and (c) pre-emption (of a partner still absent by a different bird of the same sex, which had appeared earlier). We like to add to that some more theoretical proceedings: (4) expulsion (of one pair-partner by the other one), (5) sickness (of one partner, which indeed does not lead to death), and (6) pair-expulsion (a pair is expelled by another one). These six possibilities will be examined for the barn owl following our observations:

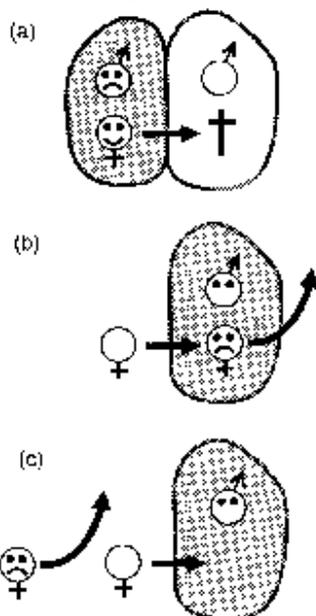


Figure 9: The different social reasons for divorce (from Ens et al. 1996: 349)

Procedure (1): To abandon a mate and to mate again during the following time seem to be clear by procedure and internal logic. At least theoretically this is not true. The mostly accepted variant is: The mate is abandoned because it is intended (variant (1a)). The reasons and the proceeding are described above. We indeed may imagine that one mate during winter time strolls about outside the borders of the original range and so

detects by hazard a possibly better partner with better resources. (The tendency to enlarge and as well to displace the home range after a brood has been described by Brandt (1992, 1995) following telemetric studies.) Him/her stays and pairs newly. Only then the separation from the former partner has been fulfilled (1b). In both variants the abandoning bird afterwards no more is at the former breeding place, the abandoned one mostly is. As the ♂ mostly even after a divorce still are at their former breeding site (see above), they preferably should be the abandoned ones. Surely this is fact in the divorce-second-broods in which the ♀ deserts her mate and their young, which are far from being independent, in favour of a new brood with a new mate (Altmüller 1976, Roulin 2002, Kniprath et al. 2004, Kniprath & Seeler 2005). Yet the possibilities are not exhausted. Rarely both partners abandon their former breeding site (Seeler pers. comm.) (1c). They obviously desert mutually. Here indeed we could interpret the situation as a not recognized expulsion of a pair by on other one (s. (6)) which then lead to divorce.

Procedure (2): Generally both sexes might be expelled from their breeding site by a third bird of the respective sex. Subsequently they are no more there. This possibility too is mostly unlikely for ♂. Also after divorce they mostly are fond at their former breeding site. For ♀ this possibility is more relevant, as after divorce they mostly are found at a different breeding site (Kniprath et al. 2004).

Procedure (3): As long as one partner after an eventual absence during winter not has returned to the old breeding site a third bird of the same sex might be earlier and mate in his place to the already present bird. This possibility too may be rejected for both sexes as barn owls stay during the winter in their breeding area and live in permanent partnership (Kniprath & Stier-Kniprath 2009).

Procedure (4): When one partner is expelled by the other one we generally may assume that the expelling one stays, the expelled one moves. Even if the divorced ♂ mostly stay at their former breeding place, the ♀ in contrast move (see above), we can by reasons of body mass (the ♂ are a little smaller than the ♀) hardly imagine that the ♀ might be expelled by the ♂. In addition we know from Epple (1985) that the ♀ as well at the beginning of courtship as at the end of the brood demonstrate an aggressive and dominant behaviour against the ♂. Because of the greater portion of staying ♂ on the other hand expulsion by the physically indeed capable ♀ mostly is unlikely.

Procedure (5): One partner temporarily fails during the brood. This variant already described above may lead to divorce but not necessarily.

Procedure (6): A pair is expelled by another one. This could lead to the divorce of the expelled pair. As barn owls do not defend a territory but only a breeding site (Glutz & Bauer 1994), the expelled pair could occupy a neighbouring breeding site. Data are not known.

Conclusion: The procedures thought as possible (+) or rejected (-) for the sexes are summarized in table 3. For the ♀ desertion of the ♂ is possible as a rare variant. We hardly believe expulsion of the ♂ by the ♀. A little more probable is mutual desertion. All other variants seem to be rather unlikely. For the ♀ expulsion by the mate is neither observed nor probable. Pre-emption is unlikely as both partners stay in their home

range over winter. All other variants are possible. Desertion of the ♂ by its ♀ has been observed between years and within seasons.

Table 3: The proceeding variants (1) - (4) of divorces in the barn owl as estimated probable (+) or rejected (-): 1a: "Intended" abandoning; 1b: "hazardous" abandoning; 1c: mutual abandoning; 2: expulsion by a third owl; 3: pre-emption; 4: expulsion by the mate

	1a	1b	1c	2	3	4
♂	+	-	+	-	-	+
♀	+	? (-)	+	+	-	-

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Summary

For a barn owl nest-box population in Lower Saxony/ Germany (520 broods) the pair-relations and their alterations (mate fidelity – divorce) were studied 1996-2009 by ringing and control of the adult birds (82%). The alterations were judged – differing from the literature – on the basis of pair-cycles (= number of the double breeding cycles following each other, which both pair partners live) with the aim to include the concerning data within the breeding seasons. We found 91 of those pair-cycles. In 78% of these the pair partners remained united. Divorces happened in very good as well as in adverse years but not in the other ones. A minor success was not proven as reason for divorce. As all divorced ♀ dismigrated for their following broods, whereas the major portion of the ♂ stayed at the former breeding site, we may suppose that concerning divorce the ♀ are the more active sex. No greater portion of divorces was found for yearlings. Divorced owls found a new mate as quickly as widowed ones. As divorced owls astonishingly often (in 5 of 21 cases) later paired again and as these in several cases for this new marriage divorced from their "interim-" mates, a personal level in the divorce reasons is less probable.

The probable issues of the divorce events are discussed enlarging the schema of ENS et al. (1996: 349). Desertion seems possible for both sexes, hazardous desertion perhaps for the ♀, pre-emption is unlikely for both sexes are resident, chasing out by an intruder is imaginable for ♀, and being propulsed by the mate only for ♂.

There were found no indications for an increase of fitness by divorce.

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