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Partnerships in the barn owl, *Tyto alba*

Summary
Frequency and function of successive and simultaneous biandry (the first term should be omitted in favour of "inner seasonal successive monogamy" ISSM), bigyny, cooperative bigamy (helper) and divorce in the barn owl are described and declared as exceptions of the life long monogamy in this species. Bigyny and ISSM occur in connection with a very good food supply. Only ISSM is sufficiently frequent to contribute to the maintenance of the species. Simultaneous biandry has not really been proved for *Tyto alba guttata* and *T. a. alba* in the field, but has been seven times for *T. a. pratincola*. Cooperation has been described once. Both could be strategies for very adverse times.

1. Introduction

Barn owls are generally socially monogamous, i.e. one ♂ and one ♀ occupy in very different manners in the production and the rearing of their offspring (BRANDT & SEEBAß 1994, MEBS 1987, GLUTZ VON BLOTZHEIM & BAUER 1994). This monogamy principally lasts as long as the two partners live (MEBS 1987, KNIPRATH 1999), hence depending on the known short longevity of the species mostly only for one brood or for the 1-2 (3) broods of a year.
Here the deviations from this principle will be described systematically following the literature, augmented by results from our study areas. Following the inner logic, these two sources will not be separated, thus leading to a better understanding. In each case, these two sources are made distinguishable. All results from our study areas are based on individually marked birds. This study does not deal with genetic monogamy, i.e. the exclusive parenthood of one ♂ and one ♀, as it cannot be studied by banding.

2. Material

The authors have been carrying out regular controls of three study areas in south-eastern Lower Saxony for several years (KNIPRATH / STIER: northern part of the district of Northeim :7 years; SEELER / SCHEMMEL: region Wolfsburg, Helmstedt, Gifhorn: 25 y.; ALTMÜLLER / KÖNEKE (part of the district of Celle). In these areas almost all pulli and tendencially all, in reality up to 85% of the adult birds have been controlled / ringed.

3. Deviations from monogamy

3.1. Biandry

3.1.1. Simultaneous biandry

Biandry in the classical sense (=simultane b.: EPPLE 1994) means, that both ♂ participate genetically in the clutch and actively in rearing the brood. Real proofs for it do not exist, only indications. The best known indication which can be found in recent books (SCHNEIDER 1995, GLUTZ VON BLOTZHEIM & BAUER 1994) originates from SCHÖNFELD & GIRBIG (1975). There we find that in the church of Haardorf, where at that time two known (banded) owls reared a brood, a second ♂ was caught. This one passed the day in a distance of only six meters above the brood. A participation in the brood was not proved. ROULIN (1996) describes eight biandrous ♀, without any comment. The agreement of numbers makes one suppose that he speaks of the cases of successive biandry cited later. Among 391 broods of *T. a. pratincola* (in northern Utah in the USA) Marti (1994) found seven cases in which two ♂ were present, some times all three bird together in the box. Only one of these biandrous trios produced eggs, but no young were reared.
A brood in Vordorf (SEELER / SCHEMMEL study area) in 1997 was successful until the fledging of the young. Here two ♂ were caught simultaneously in their box, in which the ♀ was breeding during the trapping action. The two ♂ must have entered the box together, for they were both in the trap. Both were identified without doubt as ♂, as being breeders before, or after in the vicinity. The barn owl population was down to a minimum that year.
The b- ♂ of both captivity-groups of EPPLE (1985), consisting of two ♂ and two ♀ each, both copulated with the breeding ♀ and also participated in nourishing the brood. Thus the behaviour pattern of the barn owl allows simultaneous biandry, but it still must be proved in nature by the observation of a copula, or by genetic test of all participating birds and their offspring. Concerning the study of EPPLE it must be added, that the two ♂ of each of his groups were brothers. They had established a stable hierarchy. By that the access to the respective a- ♀, which alone bred, was regulated. The a- ♂ copulated at least twice as often as the b- ♂. The ♂ also shared in supplying the ♀ with food, where the dominating ♂ fed more often, occasionally even got the prey from the b- ♀ and rendered it to the breeding ♀.

3.1.2. Serial / successive biandry

Obviously the only frequent deviation from monogamy in *Tyto alba* is the serial (following EPPLE 1994) or successive biandry (following GLUTZ VON BLOTZHEIM & BAUER 1994). Here the ♀ deserts the half-grown chicks and leaves the further rearing of the brood to the ♂. She then produces a further brood with a new mate. Both broods overlap in time (ALTMÜLLER 1976, TAYLOR 1994, ROULIN 1996). That this behaviour of barn owls has found only little attention in the literature, might be due to the fact that it is distinguishable from a normal overlapping brood (in which the pair makes both broods together) only by consequent capture of all adult birds.
The case described by ALTMÜLLER happened in 1974, the first year after a total fall in the population. A second case in the same study area was registered 1980 under very similar circumstances. During the following regeneration of the barn owl population lasting to 1984, a third case happened in 1983 but this one certainly remained an attempt. The new partners were caught being together, but no brood could be proved.
TAYLOR (1994) mentions two such bigynies, and ROULIN (1996) describes altogether eight cases, each four in 1993 and 1995, both years with a high level population. The young of the resp. first brood were between 21 and 65 days old, 48 days as mean. The new broods were at a mean distance of 3,6 km (min 1 km, max 8,5 km) from the first ones. A probable additional attempt was documented by the capture of a further ♀ together with a new mate at 8 km from her brood. This case indeed

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could be interpreted as an attempt for extra pair copulation (EPC).
Concerning successive biandry there exist 25 well-documented examples from the areas of SEELER / SCHEMMEL (22) and KNIPRATH / STIER (3). Those of the area Wolfsburg / Helmstedt from the year 1998 distinguished by the fact, that in 7 of the 16 cases of that year the ♂ had been caught before in boxes and then had been identified as non breeders (as one of them had already been in 1997). Here 1999 the hitherto unique ♂ of such a relation was found which in the same year had already reared a brood. Twenty-two of the cases were recorded in years with intensely rising- or very high owl-populations (1993, 1998, 1999, 2001), only three in the catastrophic year 1997. Here indeed the vole population had increased already in the second half of the year. This increase obviously has been a special stimulus: A ♀ had been caught during an additional attempt between two successful broods. Five weeks before the second successful brood she was found together with a third ♂ in a box, 3 km from her first and 5 km from her second breeding place.

3.1.3. Kooperative biandry
If a second ♂ is tolerated in the vicinity of a brood or even in the box, he might be a helper (= cooperative biandry after EPPLE 1985) (see below).

3.2. Bigyny
Bigyny on one hand means that one ♂ monopolizes two ♀ (EPPLE 1985). On the other hand it means in the barn owl, that this ♂ alone is responsible for the provision of both ♀ and of both broods. These broods often overlap or respectively occur parallel (=simultaneous b.). Breeding of the two ♀ belonging to one ♂ in the same box (=monolocal) twice has been stated by B. HANCOCK & S. CHINDGREN (after MARTI 1990) in captivity. SCHÖNFELD & GIRBIG (1975) describe a case of simultaneous bigyny for *T. a. guttata* for the very good year 1971. These broods were at a distance of 4,5 km (=bilocal). The observation of DE JONG (1995) refer to the same sub-species : In the Netherlands in two boxes hanging 2 m apart in two consecutive years two ♀ raised a brood with the identical ♂. All three birds in both years were identical (DE JONG, pers. comm.). ROULIN (1996) documents for 1994 and 1995 (successful years both) three and two (resp.) attempts of bigyny, mean distance 1,2 km (min 0,5 km, max 1,5 km) from the actual brood. Elsewhere three cases of bigyny have been reported. MARTI (1990) found four cases of bigyny for *T. a. pratincola*, i.e. four trios (one ♂ and two ♀ each). One of these trios disappeared after laying two eggs, in another one, one of the ♀ disappeared already during egg-laying, or during incubation. The then remaining pair of this trio reared two broods that year. The other two trios successfully reared young until fledging. In these cases the two ♀ brooded in the same box in close vicinity, in one case so narrow that MARTI could not assign the 13 eggs to one of the ♀ (the volume of the box would have allowed the two ♀ to brood distinctly apart). MARTI found three of these cases in 1987 and one in 1988. He estimates neither a lack in breeding sites nor a biased sex ratio as being the cause.
Unmarried barn owls were rarely found and the sex ratio of carcasses was not significantly different from 1:1. Also the regimen as judged from the pellets did not differ from that of monogamous pairs of the region. The ♀ engaged here were clearly less successful than the monogamous broods controlled simultaneously by MARTY. The success values of the ♂ too were below those of the monogamous ones. Additionally Marti found a marked ♂ which roosted alternately with two different ♀ at a distance of 400 m. Furthermore he estimates about 10% of the broods, which he did not succeed in catching a ♂, as bigamy candidates.
TAYLOR (1994) recorded seven cases (among 419 broods / brood attempts) in *Tyto a. alba*, " Usually the two females were in separate nest sites up to about 1 km apart and one of them received much less food than the other and consequently was less productive. The single notable exception involved two females who laid clutches of four and five eggs only centimetres apart so that during incubation they were nestling with each other. From each clutch only one young was fledged." TAYLOR also describes, how bigyny may establish: "However, even during the breeding season, new females sometimes appear, spending anything from a few days to a week or two roosting alongside the incubating female. Very occasionally this association goes a stage further and the second female is mated by the male and produces a clutch."
SHAWYER (1998) describes, also for *Tyto a. alba* three cases and emphasises that bigyny only happens if prey is abundant. Two of these bigynic broods took place two years apart in the same building. Concerning the third one, two ♂ supplied three broods under the roof of a very large farm house. SHAWYER writes: "Bigamy seems to be especially common with barn owls which had originated from captive stock having successfully been released into the wild."
BUNN, WARBURTON & WILSON (1992) found only one case (as well for *Tyto a. alba*) under artificial conditions. A ♂ was fed ad libitum with first day chicks and took the chance to make a further brood with a second ♀ at the same time. MARTÍNEZ & LÓPEZ (1999), who emphasise the uniformity of prey abundance in southern Spain, could directly observe one case (*T. a. a.*). The two broods were at a distance of 40 m and from both five young fledged.
In the southern Lower Saxony study area (Kniprath / Stier) up to 2001 among 270 broods two certain cases of bigyny were found (one in 1998, a year with intensely rising owl population and one in 2001 with maximum owl density). The broods in 1998 took place at a distance of about 450 m in a village, in which a monogamous pair reared a brood simultaneously. The bigynous ♂ could fly to and fro between his two broods without touching the narrower range of the third brood. The two broods in 2001 were in a distance of less than 200 m. One more case was detected in the SEELER / SCHEMMEL study area. In Velpke, Helmstedt district, a couple (♀ 1, ♂ 1) had deserted its first brood. The pair successively made a replacement brood in a different box in the same village, about 500 m apart. About nine weeks later, at a distance of 2,2 km, ♂1 began a new brood with ♀2, which had been found breeding earlier in the year at a different place (♂ 2). To summarize: four owls made in the course of one year one attempt, one normal brood, two bigynous broods (♂ 1 with ♀ 1, ♀ 2), and two successive biandrous broods (♀ 2 with ♂ 2, ♂ 1). This is a unique

case among the hitherto about 1030 broods of that study area and happened in 1998, a year with a heavily mounting barn owl population.
Possibly bigyny was found in 1991 in the ALTMÜLLER / KÖNEKE area: Two ♀ were caught at a brood with recently hatched chicks after an interval of two days. The ♂ was caught only at the second attempt. Four weeks later nothing had remained of this brood. The ♂ later had a replacement brood with a third ♀.
Not to far away from these areas (16 km north west from Hannover) BOENIGK (2000) could follow the events in a bigynous brood by controlling the box every 2-5 days. A widowed ♀ with 4 eggs had attracted a new ♂, which now fed her with prey. Four day later, in the same box a second ♀ was detected having 2 (later 3) eggs. The two clutches were 70 cm apart. Both hatched and fledged successfully (3 and 2 chicks).

3.3. Helpers

As already mentioned in the chapter biandry, trios can function in such a manner, that a third bird simply acts as helper. Certainly this was the case in the four bird groups of EPPLE (in captivity, see above). Here the b- ♀ did not participate in the clutch production. In one group in contrast she was expelled by the a- ♀ from the brood site during the laying period. Covering the clutch, too was done solely by the respective a- ♀. Both b- ♀ later participated – even in not too great an extent – in providing the broods, i.e. they rendered prey to the a- ♀. They were not allowed to feed the chicks.
Aggressiveness like here in captivity was not observed in the wild MARTI (1990), TAYLOR (1994), and BOENIGK (2000), where the ♀ breeding closely together had a peaceful association.
A helper in the wild was observed in the KNIPRATH / STIER study area in 1993. A ♀ not known before (the ♂ was not caught) was aided in nurturing by an additional ♀, which had its own successful brood at a distance of 3,4 km. In the ALTMÜLLER / KÖNEKE area there was an otherwise unobtrusive brood in 1991, where two ♀ were caught. One of these could have been a helper.

3.4 Divorce

If, as seems to be sure, life long monogamy is the rule, divorce is one of the interesting exceptions. To define exactly: We only speak of divorce, if after a brood (an attempt) at least one partner begins a new partnership as long as the old mate is still alive. (In this sense, the successive biandry described above is preceded by a divorce.)
Very little can be found in the literature on divorce with new partnership of both mates. MARTI (1994) could document two cases. In each of them both divorced partners brooded in the following year with a new mate at different sites. None of them stayed in the original site.
In their study areas the authors found examples for the divorce of successful pairs from one year to the next. In the ALTMÜLLER / KÖNEKE area the partners of a brood of the year 1977 were found again in the next season, each with a new mate. After divorce both moved to a new village (3,7 and 2,6 km). In 1991 too there was a divorce. The ♂ remained and the ♀ moved for 5,5 km.
In the KNIPRATH / STIER area we found five divorces which in part will be described in more detail, as they illustrate some more events which would be overlooked when only numbers were given. Three of these divorces belonged to a single ♂.
From 1993 to 1994 there was the divorce of Christian and Berta (we name the birds to facilitate recognition for the reader and the writer). Christian brooded in 1994 in the same box together with Cheryl, an earlier daughter of Berta, but not of Christian. Berta was not found that year. In the next season (1995), the original partners Berta and Christian brooded again together (in a different box in the same village), hence remarriage. (Berta is the helper mentioned above.)
In this case the circumstances also allow a different interpretation. Cheryl's 1993 brood took place in the next village, only 1,5 km apart from the brood Christian / Berta. Her mate was not caught. Christian could have been the father of this brood,e too. In that case he had not changed mate from 1993 to 1994, but had brooded in 1994 with one of his former mates. The assumption of a bigyny in 1993 is not too fantastic as 1993 in that area was a very good barn owl year.
In the same area Felina and Fasold divorced after their brood of 1996; Fasold stayed in the village and brooded 1997 in a different box with Gudrun. Felina in 1997 was found breeding in Fallersleben (85 km NE in the SEELER / SCHEMMEL area). From 1997 to 1998 Fasold and Gudrun divorced too. They both moved away in different villages (Fasold 2,1 km, Gudrun 10,2 km). Fasold brooded in 1998 with Hanni. From 1998 to 1999 Fasold had his third divorce. Hanni stayed and brooded with a new mate, Fasold moved and brooded only 1,8 km apart. Hanni hitherto is the only ♀ to stay at her breeding site after divorce.
The number of divorces in the SEELER / SCHEMMEL area seems unusually high. From 1994 to 2001 for 49 pairs both partners were caught again in the following year (= 49 pair years). Thirty of these pairs remained together, 19 had divorced. In nine of these cases, both partners had left their breeding site. In the remaining ten the ♂ stayed, the ♀ moved. The inverse case – ♀ stays, ♂ moves – was not found. There was no individual divorcing twice.
Here too a remarriage was found: The partners of a pair 1992 in Velstove were found together again three years later, even in the same box. For the ♀ brood had been proved in both years between these dates, both times in Velstove, 1993 with a different ♂, 1994 in the same box. In the latter year no ♂ was caught, Remarriage therefore could have taken place already in 1994 and not in 1995.

4. Discussion

For the barn owl lifelong monogamy obviously is the most advantageous solution for normal years. Mate fidelity from one season to the next is advantageous for both sides. The ♀ knows the qualities of the ♂ as hunter and needs no long trial period. From this an early breeding disposition may result with the advantageous chance of adding a second brood if other circumstances remain positive. By the reduced courtship the male serves energy, which he can later invest in providing for the family.

Special circumstances promote special strategies.

If the times, i.e. the prey abundance, are especially adverse, simultaneous biandry may be advantageous for all birds concerned. For the ♀ the situation is immediately understandable: For her, provision by two ♂ increases the chance, that her brood could be successful even under these disadvantageous circumstances (in this sense also discussed by EPPLE 1985). For the two ♂ the calculation might be like this: Individually none of them might have stimulated the ♀ to breeding. The result would have been total brood cancellation, say zero-success (so also SCHNEIDER & SCHNEIDER 1928, SAUTER 1956, BÜHLER 1964). But so there is a real possibility that the proper genetic material will survive at least in one or other of the offspring commonly raised. Calculating the low longevity of the species, waiting for a better chance in the following year would be a lesser strategy.
If in contrast times are very good, bigyny is well-understandable. In normal seasons power and time of a ♂ are insufficient to provide two broods. Probably both would not be very successful. "Paradise like" vole quantities all around reduce the amount of power and time needed for a single brood, so that enough of both remains (EPPLE 1993). The proof of bigyny in southern Spain (MARTÍNEZ & LÓPEZ 1999) could be explained by the permanent good prey situation there. This interpretation is supported by the occurrence of 33% second broods.
It could be presumed that successful bigyny clearly increases the fitness of a ♂, for he has not to survive a risky winter to make a new attempt. In contrast to that, MARTI (1990) found for *Tyto a. pratincola* that the bigyneous ♂ were less successful than the monogyneous ♂ of the same period. For a ♀ bigyny is the best solution, if a mate for a monogameous pair bond is lacking. Indeed it is hardly to be proven, whether this applies to the concrete case. Concerning his cases, MARTI (1990) does not believe that there was any lack in ♂ . The interpretation as a second-best solution is supported by the observation of MARTI that the two ♀ of the bigyneous ♂ were less successful than those of the monogameous ones of the same period. Furthermore, MARTI does not find any convincing explanation for the bigyny observed by him and moreover, for his area he can exclude only one possible reason for the breeding of two ♀ in one box: the lack of breeding sites.
The term, a ♂ "monopolizes" two ♀ (EPPLE 1993) assigns the ♂ an active role. That must be doubted considering the association of two ♀ described by TAYLOR (1994). The latter can only be an active and voluntary action of the ♀. Successive biandry is the chance of the ♀, corresponding to the special chance of the ♂ being bigyneous.
A ♀ can dare it without endangering her progeny of the first brood only if the first ♂ easily provides the prey necessary alone and she is not obliged to assist. Correspondingly successive biandry is observed first in years with abundant prey. This strategy raises the fitness of the ♀, which in shorter time produces more offspring (longevity!). Obviously it means gain in fitness for the second ♂ too. For most of these second ♂ this brood is the sole one of that year.
But also a different interpretation of the successive biandry seems possible. As it always (for the ♀) shortens the distance between two broods, an eventually in later summer occurring severe decline of vole numbers could be prevented. Such a crash would eventually harm a late regular second brood of the original pair (even if it would overlap with the first one) and let it fail. This interpretation may be continued: Is that the way to make the (few) third broods (as, for example, described by OTTEN 2000) possible?
Epple (1985) states for all pairs observed by him in the wild and even more in captivity a tendency "to deliberate the ♀ from parental duties towards the end of the elevation phase". He interprets that as "adaptation in the connection with the ability to breed repeatedly". "Already OTTENI, BOLEN & COTTAM (1972) point to this job sharing as supposition for second broods" (quotations from EPPLE 1985). What is considered right for second brood generally should be the more so for biandreous second broods.
The term "deliberate" could infer that here we see activity from the ♂. But it seems more likely that the ♀ may ascertain by the reduction of her feeding performance whether the ♂ is able to feed the brood alone. Only then – and obviously only if there is an unmated ♂ not too far away – she can "say good-bye". A successive second brood indeed mostly enhances the ♂ to have a second brood, but quite helps him in providing his descendants with food as the ♀ needs no more be nourished from the same territory. The ♀ on the other hand – by the aid of her new ♂ - now can use resources in quite a larger distance from her first brood.
Here it seems useful to have a closer look at the definitions "serial biandry" (EPPLE 1994) and "successive biandry" (GLUTZ VON BLOTZHEIM & BAUER 1994).
With the exception of a few cases of bigyny and real biandry (see above) barn owls are socially monogameous: One ♂ and one ♀ produce together a clutch and care for the offspring at least up to an age of 3-4 weeks. Being real monogamy is independent of the time, the ♀ shares providing the pulli. From the beginning of the second brood on, may it be with the first or a new mate, according to our knowledge, all participation of such a ♀ in her first brood ends. And also in the case of the second brood it is without doubt monogamy (as it is in a new brood after a winter). Not the distance between two broods (or participations) decides whether it is monogamy or not. But as here a ♀ never participates simultaneously in two broods, or on the other hand two ♂ share the provision of one brood, it cannot be biandry. "Successive biandry" is a contradiction in itself. The term should not be used, as well as "serial biandry".
Proposed new definition:
Serial monogamy as a system is illustrated by burrowing beetles (Arthropoda, Coleoptera) and the Zebra finches (GOULD & GOULD no year). In both cases the partnership is finished, as soon as all species-specific acts for the offspring are done. For a new brood the partners unite newly totally independent from the former ones. BAEYENS (1981) also uses the term in the magpie. Here individuals desert the mate after a failed brood and newly mate an unmated (or widowed) bird if he is owner of a better territory.
Even if not all circumstances described by the authors fit, the term successive monogamy fits exactly. It also fits for broods which after divorce take place in a following year. Here we suggest the term **inner seasonal successive**

monogamy (**ISSM**). The resulting second brood should be named **divorce second brood**.
For **helpers**, who per definition do not participate genetically in the brood, a gain in fitness is recognizable only in the case, if one of the parents of the brood is a near relative. In that case the aid would support the helper's genes, which at least in part belong to all relatives. Supposition is that near relatives know each other forever, or can recognize each other. Unfortunately the owls breeding in the study areas of the authors only in a far too small a partition are known in their origin (outside the study areas unfledged barn owls are no more banded in a greater amount) as to know clearly the relations in such interesting cases. Clarification could be reached by systematic genetic control (fingerprint). Permanent personal knowledge of relatives could be contradicted by the occurrence of a mother-son-incest (KNIPRATH 2004).
It is certainly imaginable that in the behaviour-pattern of the barn owl a smooth transition between the association described by TAYLOR (1994), the role as helper, and real bigamy exists.

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