Breeding ecology of the Barn Owl (Tyto alba) in Valencia (SE Spain)

José Antonio Martínez and Germán López

Departamento de Ecología, Universidad de Alicante, E-03080 Alicante, Spain

Summary

We studied the reproductive parameters of a population of Barn Owls (*Tyto alba*) in Valencia (SE Spain) from 1989 to 1995. About one third of females laid second clutches, but the laying date of first clutches was not different for females laying one or more than one clutch per year. Also, there were no differences in the laying date of first clutches between years. Clutch size did not vary through the season, nor between the different study years. The main prey brought to the nests was rats, which represented the 62.6% of prey biomass. The modal clutch size was 5 eggs, and larger clutches were infrequent. This clutch size also produced more fledglings per nest than smaller or larger clutch sizes. This coincidence of modal and most productive clutch size is hypothesized to be related to the stability of climate and resource supply in the study area.

Key words: diet, laying date, clutch size, breeding success, second clutches

Zusammenfassung

Brutbiologie der Schleiereule (Tyto alba) bei Valencia (SO-Spanien)

Von 1986 bis 1995 untersuchten wir die Brutbiologie einer Population der Schleiereule bei Valencia. Etwa ein Drittel der Weibchen legte eine zweite Brut. Es bestand kein Unterschied im Legezeitpunkt der ersten Brut zwischen Weibchen, die ein- oder mehrmals brüteten. Der Legezeitpunkt der Erstbrut war von Jahr zu Jahr sehr ähnlich. Innerhalb der Saison wie zwischen den Jahren variierte die Gelegegröße kaum. Durchschnittlich wurden fünf Eier gelegt. Die durchschnittliche Gelegegröße war zugleich die relativ produktivste. Dies wird als Ausdruck der im Untersuchugnsgebiet alljährlich recht stabilen Klima- und Ernährungsverhältnisse interpretiert. Mit 62,6% aller Beutetiere machten Ratten die hauptsächliche Beute aus, mit der die Jungen gefüttert wurden.

Introduction

The Barn Owl is a medium sized nocturnal bird of prey that breeds throughout a vast latitudinal range (40°N to 40°S) (Mikkola 1983). Voles form the bulk of its prey in temperate European regions (Taylor 1994), while in Mediterranean Spain the diet of the Barn Owl is based mainly on Muridae (Vargas et al. 1988), whose populations have not been shown to experience the great fluctuations (Gosálbez 1987) characteristic of Arvicolidae.

Although some generalisations about the breeding ecology of the Barn Owl have been put forward (Muller 1991, Taylor 1994) (for instance about annual variation of laying dates, seasonal variation of clutch size and an hypothetical latitudinal gradient in the frequency of second clutches), they have been based on results obtained mainly in Central and Northern Europe, while studies from Mediterranean countries are lacking (Muller 1991, Taylor 1994). Most published studies have described the main reproductive parameters of the Barn Owl, but little attention has been paid to the relationship between clutch size and breeding success, despite this being one of the aspects of life history theory that has stimulated most research and discussion (Stearns 1992).

The aims of this paper are (1) to describe the breeding phenology of the Barn Owl in a Mediterranean area over a period of 7 years, (2) to examine clutch size variation within and between years, (3) to analyse the relationship between clutch size and breeding success, (4) to provide some data on diet in the breeding season and (5) to compare the breeding ecology of the Barn Owl in a Mediterranean area with that of more northern European populations.

Study area and methods

We surveyed a 19 km² area on the SW edge of the city of Valencia (0° 25'W, 39° 25'N). An additional pair from the NW edge of Valencia was included in the study population. Orange groves and small vegetable smallholdings formed the bulk of the mosaic-like landscape within a one kilometer radius of all the nests. The annual average temperature in the area is 18 °C, and the average rainfall is about 500 mm per year (Urios et al. 1991).

We monitored this population for seven years, 1989-1995. We collected data on laying date, clutch size, brood size and fledging success for each nest. In 1992 we were only able to record the number of breeding attempts. With the exception of 1992, most potential nest locations were inspected to check for the presence of the species. Once the female was observed frequently roosting in one accessible cavity, it was checked at least every second night. Thus, most clutches were found during the laying period (36 out of 39 clutches). Five nests were found containing nestlings, the ages of which were estimated according to Taylor (1994). Laying date was estimated on the basis of the fact that Barn Owls normally lay one egg every two days (Taylor 1994). Nests were inspected when the females left for a short while to take prey from the male or simply to fly around the nesting area. Nestlings older than 36 days, the earliest age at which young Barn owls attain maximum weight (Taylor 1994), were considered as fledglings. We checked nests after the young had flown to search for remains of dead nestlings. All the nests were located in empty niches of cemeteries (coffin-shaped cells for burying the dead, measurements $2.3 \times 0.9 \times 0.9$ m, arranged in four tiers. Owls bred on the fourth level beyond the reach of passers-by). Six second nesting attempts occurred in inaccessible nests, precluding monitoring of breeding parameters. Nevertheless they were taken into account in the counting of second clutches.

We took pellet samples from the ground for only 3 different nests, because most pellet accumulations were not accessible owing to the structure of nesting sites in cemetery niches.

Since the pattern of primary feathers is unique to each bird, we collected each year all moulted primary feathers in the niches and used them for the identification of individual females (Taylor 1994). As an aid, we performed several identification trials using annual sets of slides and blind tests with sets of feathers of captive birds. Unfortunately, we could not identify males, which were very seldom seen at the nests (1.25% of the diurnal visits, n = 560).

Results

Diet

The main prey was *Mus* sp. representing 41.4% of 533 identified items, followed by *Rattus* sp. with 30.8%, *Crocidura russula* (11.4%), Passerines (11.3%), Chiroptera (3.4%) and *Apodemus sylvaticus* (1.3%). When data were transformed to biomass (Gosálbez 1987, Jiménez et al. 1989), *Rattus* sp. contributed the largest percentage of the total intake (with 62.6%) and *Mus* sp. the second largest (with 20.6%).

Timing of laying and clutch size

In the main study area (SW of Valencia), we found seven Barn owl pairs (density 0.36 pairs/km²). Out of the eight breeding territories monitored in the whole study area, we were able to identify seven females by distinctive patterns on their primary feathers (Taylor 1994). One female was not individually identi-

fied because moulted primaries could not be collected. Six out of the seven identified females survived and bred in the same territories throughout the study period (7 years). One disappeared after three years, and presumably died.

The total number of breeding attempts found was 63 (63.5% first clutches, 28.6% second clutches, 7.9% third clutches, 0% replacement clutches). The percentage of pairs laying second clutches was: 1989, 28.6%; 1990, 60%; 1991, 33.3%; 1992, 40%: 1993, 0%; 1994, 40%; 1995, 40%. Third clutches occurred in 1989, 1990, 1992 and 1995, one each year except in 1992 when 2 pairs laid third clutches. The weighted averages for all years were 53.8% of pairs laying only one clutch, 33.3% laying a second clutch and 12.8% laying a third clutch.

Laying date was determined in 44 cases. The earliest Barn owl clutch was laid on 13 February (1989) and the latest on 22 December (1990). The mean laying date for first clutches was 9 April (n = 34, s.d. = 27.18 range: 13th February to 23th June), for second clutches 30 July (n = 7 s.d. = 50.14 range: 29th May to 10th October) and for third clutches 10 November (n = 3 s.d. = 39.21 range: 5th October to 22th December).

The average interval between the laying of the first egg in first and second clutches was
 Table 2. Seasonal variation of the average clutch size (all the years pooled) of the Barn Owl in Valencia.

Tab. 2. Saisonale Variation der Gelegegröße (alle Jahre zusammen) der Schleiereule bei Valencia (Spanien).

Months	Clutch Size	s.d.	n
March-April	4.78	1.49	23
May–June	3.62	1.41	8
July-September	4.50	0.58	4
October-December	4.33	0.58	3

99.3 \pm 42.4 (s.d.) days (n = 6, range 79–185). On four occasions females begun a second clutch while fledglings of the previous brood were still not independent. There was no difference in the average laying dates of first clutches between females (all years pooled: F_{5,24} = 0.45, n.s.) or in the average laying dates of first clutches between years (F_{5,24} = 0.92, n.s.). Pairs that laid second clutches did not begin breeding earlier than those which only laid one clutch (F_{1,42} = 1.32, n.s.).

Clutch size was determined in 39 cases (30 first clutches, 7 second clutches, 2 third clutches). The average size of first clutches was 4.63 \pm 1.40, 3.86 \pm 1.35 for second clutches, and for third clutches 4 \pm 0). The sizes of first and second clutches were not significantly different (F_{1,35} = 1.76, n.s.). The overall average was 4.46 \pm 1.37) and the overall mode was 5

Table 1. Clutch size variation for the Barn Owl in Valencia, and the production of fledglings per nest, calculated both with all the data and excluding the total losses.

Tab. 1. Variation der Gelegegröße und des Bruterfolges der Schleiereule bei Valencia (S	panien). Der Bruter-
folg ist zum einen für alle Bruten, zum anderen nur für erfolgreiche Bruten dargestellt.	

Clutch size	Frequency	Fledglings/nest (all data)	s.d.	Fledglings/nest (excluding total losses)	s.d.	Number of nests with partial losses	Number of nests with total losses
1	1	1	_	1		0	0
2	3	2	0	2	0	0	0
3	2	3	0	3	0	0	0
4	11	2.45	1.44	2.70	1.25	2	1
5	18	3.74	1.73	4.18	1.18	3	1
6	1	1	—	1.45	_	0	0
7	1	2		2.45		1	0
9	1	4		4	_	1	0

Table 3. Yearly averages of laying date of first clutches (1st c.), clutch size (all clutches, all c.) and fledglings produced per nest.

Tab. 3. Mittlerer jährlicher Legezeitpunkt der ersten Brut (1st c.), Gelegegröße (alle Bruten) und flügge Jungvögel je Nest der Schleiereule bei Valencia (Spanien).

Year	Laying date (1 st c.)	s.d.	n	Clutch size (all c.)	s.d.	n	Fledglings/nest (all c.)	s.d.	n
1989	28-March	24.38	7	4.2	1.56	9	2.56	1.33	9
1990	10-April	31.38	5	4.0	1.41	10	5.00	1.32	9
1991	20-April	29.51	6	4.6	5.53	7	3.57	1.72	7
1993	26-April	30.88	6	5.5	1.76	6	4.33	0.82	6
1994	25-March	5.36	5	4.8	0.45	5	3.83	1.60	6
1995	8-April	27.18	5	3.5	2.12	2	3.50	1.76	6

(48.7% of all clutches, Table 1). The mean clutch size of first clutches for females laying only one clutch was 4.93 ± 1.41 (n = 15), and for those which laid second clutches 4.00 ± 1.56 (n = 10), the difference not being significant (F_{1,23}= 2.36).

There was no difference in the average size of first clutches between females ($F_{5,22} = 0.77$, n.s.) or between years ($F_{5,24} = 0.92$, n.s.). The clutch size was fairly constant throughout the year (Table 2), and no significant relationship between clutch size and laying date was found (r = -0.124, df = 37, n.s, all years pooled).

Excluding 1995 (a year for which only two clutch sizes are known) the mean yearly clutch size varied from 4 (1990) to 5.5 (1993) (Table 3). No relationship was found between annual average laying date and average clutch size, either for all clutches pooled (r = -0.605, df = 3, n.s.) or for first clutches only (r = 0.447, df = 3, n.s.).

Polygyny was detected once (1.7%), as evidenced by the male hunting in the vicinity of two nests and delivering prey to both of them (40m apart), and by the two females feeding their broods simultaneously. Both clutches were considered as firsts, and five fledglings were successfully raised in both nests.

Hatching and fledging success.

A hatching success of 83% was determined for 174 eggs from 39 nests. Fledging success was determined in 44 nests. The average fledgling production for first clutches was 3.32 ± 1.59 fledglings per nesting attempt (n = 34), for second clutches 2.43 \pm 1.62 (n = 7), and for third clutches 2 \pm 2.00 (n = 3). We found no significant difference in fledging success between first and second clutches (F_{1,39} = 1.83, n.s.). All of the nestling mortality recorded occurred within the first 36 days after hatching.

The number of fledglings produced per nesting attempt in relation to clutch size is shown in Table 1. The most productive clutch size was 5 eggs. This clutch size fledged significantly more young than clutches of 4 eggs ($F_{1.26}$ = 11.92, p < 0.01) and than clutches of 6 to 9 eggs pooled ($F_{1,18}$ = 5.75, p < 0.05). The maximum number of fledglings produced by clutches with more than 5 eggs was 4, while the 56% of clutches with 5 eggs produced 5 fledglings.

Only two cases of total nest failure were recorded (Table 1). One was due to the desertion of a clutch of 5 eggs by a female that disappeared from the area. Next season only one Barn Owl was observed in this cemetery and no breeding attempt was observed, so we assume that this desertion was probably due to the death of the female. The other total failure happened to a third clutch, whose nestlings were found dead after heavy autumn storms. Unhatched eggs and partial losses of nestlings were only found in clutches with 4 or more eggs (Table 1).

Discussion

The laying dates of first clutches of the Barn

owl in our study area did not show any significant variation between years. In Scotland, however, Taylor (1994) found between year variation in laying dates that was best explained by variations in prey abundance, mainly *Microtus* voles. In the Netherlands, De Jong (1990) also found a relationship between laying date and density of the common vole (*Microtus arvalis*). In other owl species breeding in the North of Europe, such as Tengmalm's owl (*Aegolius funereus*; Korpimäki 1986) and Ural owl (*Strix uralensis*; Pietianen et al. 1986), a negative correlation was also found between spring vole abundance and laying date, meaning that early laying occurred when food was abundant.

Clutch size did not vary significantly between years or between females, and was fairly constant throughout the season. Different results have been obtained elsewhere. Taylor (1994) found wide variation in clutch size both between years and within years in Scotland: years with early laying dates were also years of high clutch sizes and, within years, early laying pairs produced the largest clutches. Marti (1994) also found a seasonal decline in clutch size in Utah. In central Europe (Schönfeld & Girbig 1975, Baudvin 1986) and Mali (Wilson et al. 1986), clutch size increased at the beginning of the season, peaked in June-July, and then declined. Taylor (1994) linked the two patterns to changes in main prey availability. No seasonal pattern of clutch size variation was found in our study area; clutch size was constant throughout the year. Barn Owls in our study area fed mainly on Rattus sp. in suburban habitats (Jiménez et al. 1989), whose numbers are probably not subjected to the strong fluctuations frequent in other rodent species (Gosálbez 1987). This fairly constant food supply could explain the constancy of clutch size throughout the season observed in this area.

The Barn Owl can produce up to three broods per year, and the period between laying of eggs and independence of the young is rather long (120 days; Bunn et al. 1982). Thus, the Barn Owl is likely to benefit from starting laying as soon as possible, thereby enabling it to produce as many young as possible (Taylor 1994). It has been suggested that in continental European populations natural selection would favour early laying even if it meant laying fewer eggs in first clutches (Taylor 1994). This would allow females to lay second clutches. This pattern has been observed in several European localities, where only pairs that start laying well before the average of the year produced second clutches (Baudvin 1979, Muller 1991, Taylor 1994), but not in our study area where the laying date of first clutches was not different for pairs laying one or several clutches.

It was believed that the Barn Owl rarely produces second clutches in Mediterranean areas (Muller 1991, Taylor 1994). Muller (1991) suggested that the occurrence of second clutches in the Barn Owl has evolved so that it compensates for overwinter losses: the frequency of second clutches has a latitudinal gradient throughout Europe. Frequency declines southwards as the winter is milder and winter mortality lower. The fact that the frequency of second clutches in our study area, 33% on average, is similar to values found in Central and Northern Europe does not support this hypothesis.

The mean clutch size in our study area did not differ from the average of 4.67 eggs for England (t = 1.08, df = 215, n.s.; Bunn et al. 1982), but was significantly lower than the mean clutch size of 5.21 eggs in Switzerland (t = 2.57, df = 133, p = 0.011; Luthy et al. 1975) and 6.26 eggs in France (t = 5.92, df = 512, p = 0.009; Baudvin 1979). Although the modal clutch size in all these populations was 5 eggs, the proportion of clutches greater than this size varied greatly among them. So, while in the Valencia population only 7.7% of clutches had over 5 eggs, the values for the other populations were 61.9% for France, 35.4% for Switzerland and 20.8% for England.

The low frequency of clutches larger than 5 eggs in our study population could be explained if they were less productive than smaller clutches. In fact, this was the result obtained

since the mean number of fledglings per nest when clutches of over 5 eggs were pooled was 2.3, a significantly lower value than the 4.18 fledglings per nest produced by clutches with 5 eggs (Table 1). The clutches of 5 eggs were also more productive than those of 4 eggs (Table 1). Hence, in our population the modal clutch size and the most productive clutch size coincided.

Most studies have found that the most frequent clutch size is smaller than the most productive (Klomp 1970, Stearns 1976). Several hypotheses have been suggested to explain this difference. One frequently quoted hypothesis states that, owing to reproduction costs, birds maximise lifetime breeding success by laying clutches smaller than the most productive clutch (Stearns 1976, Bryant 1979), since a large investment in a present breeding attempt may reduce future survival and/or reproductive output of the parents. However, while the modal clutch size of the Tengmalm's Owl was smaller than the optimum (Korpimäki 1987), no evidence was found of reproductive costs in this species (Korpimäki 1988). The fact that six out of seven females survived for at least seven years suggests that reproductive costs, in terms of adult survival, were low or non-existent for Barn Owls in our study population.

An alternative hypothesis has been proposed that does not need to consider reproduction costs. Boyce & Perrins (1987) linked the difference between the modal and the most productive clutch size to fluctuating survival prospects of the chicks. When there are marked annual environmental fluctuations, the geometric mean is more appropriate to measure fitness than the arithmetic mean (Gillespie 1977, Stearns 1992). In fluctuating environments, individuals laying large clutches would have low geometric mean fitness if they experience great variance in reproductive success, because the geometric mean decreases as variance increases. If this is true, we could predict that birds living in fluctuating environments would lay clutches smaller than the most productive one, while in birds living in more stable environments, where variance in reproductive success would be reduced, the modal clutch size would approach the most productive clutch size.

In our study area neither average laying date nor average clutch size varied between years; clutch size was fairly constant throughout the season and did not vary between females; laying dates of females that laid one clutch did not differ from those of females that laid second clutches; pairs laid up to three clutches per year. They fed mainly upon rodent species that, unlike Arvicolidae, are not known to experience strong population fluctuations. All of these are symptoms of a stable habitat. Thus, the coincidence of modal and most productive clutch size in our study area would support the hypothesis of Boyce & Perrins (1987). On the other hand, Barn Owl populations studied in other more northern European localities feeding mainly on Arvicolidae rodents, have been shown to present between year differences in clutch size and laying date, differences in the laying date of first clutches between females in relation to the number of clutches laid per year and clutch size changes throughout the season (de Jong 1990, Taylor 1994). Unfortunately, and despite the existence of large files of data on Barn Owl breeding parameters, to our knowledge no analysis relating fledgling produced per nesting attempt to clutch size in this species has been published. However, at least for two of the European populations, the number of fledglings leaving the nest in relation to clutch size may be calculated. In Bourgogne the modal clutch was 5 eggs, while the most productive clutch was 10 eggs (Baudvin 1979). In Britain, the modal clutch size was also 5 eggs, while the clutch size that produced more fledglings, considering only broods that fledged at least one chick, was 6 eggs (Bunn et al. 1982). These results seem also to support the hypothesis of Boyce & Perrins (1987), but in order to establish the generality of this pattern this kind of analysis would need to be repeated in a broader range of localities.

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