Pakistan J. Zool., vol. 56(2), pp 533-541, 2024 DOI: https://dx.doi.org/10.17582/journal.pjz/20220210080258

The Breeding Ecology of the Boreal Owl (*Aegolius funereus beickianus*) in Gansu Province, China

Yongke Zhu[1,2], Yun Fang[1], Songhua Tang[1], Yuan Gu[3], Jinming Zhao[4], Wolfgang Scherzinger[5] and Yue-Hua Sun[1]*

[1]*Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China*
[2]*University of Chinese Academy of Sciences, Beijing 100049, China*
[3]*Department of Zoology, Tianjin Natural History Museum, Tianjin 300201, China*
[4]*School of Life Science, Huaibei Normal University, Huaibei 235000, China*
[5]*Nationalpark Bayerischer Wald, Guntherstrasse 8, D94568 St. Oswald, Germany*

Article Information
Received 10 February 2022
Revised 05 April 2022
Accepted 25 April 2022
Available online 15 November 2022 (early access)
Published 16 January 2024

Authors' Contribution
YZ and Y-HS conceived and supervised the study and had substantial inputs into the analysis and all drafts. YZ, YF, ST, YG and JZ conducted the study in the field. WS co-supervised the study and had substantial inputs into the drafts of the paper. All authors have read and agreed to the published version of the manuscript.

Key words
Boreal owl (*A. f. beickianus*), Clutch size, Incubation period, Nestling period, Breeding success

ABSTRACT

The boreal owl (*Aegolius funereus*) has a circumpolar distribution, typically inhabit extensive conifer forest of higher age classes in the northern hemisphere. Breeding biology, reproductive strategies, and behavioural ecology of these nocturnal birds are well studied in Europe and North America. However, the knowledge of the subspecies of boreal owl (*A. f. beickianus*) in the coniferous forests at high mountainous altitude of the Qinghai-Tibet Plateau is still limited. We spent 10 years studying the breeding biology of *A. f. beickianus* in Lian Hua Shan Nature Reserve (Gansu Province), where we could first confirm the occurrence of this small forest dwelling owl in 1995. During breeding seasons (2003-2009, 2017-2019), we checked nest boxes and recorded the basic breeding data. Thereby a total of 51 broods were found with an average of 5.1 ± 1.7 broods per year. The mean egg mass and volume was 12.42 ± 1.36 g and 12.85 ± 0.79 mm^3, respectively. Mean clutch size per brood was 2.61 ± 0.64. The mean number of fledglings was 1.25 ± 0.31 per nesting attempt and 2.07 ± 0.38 per successful brood. Nestling period lasted 35.75 ± 2.80 days in total, but was divided in two stages: in the first stage, which lasted 16.75 ± 1.48 days, the female stood in the breeding hole with its nestlings. In the second stage, which lasted 17 ± 4.34 days until the fledglings left their nest, the female stood outside the hole. The individual fledglings left the nesting site in intervals of 2.55 ± 1.92 days.

INTRODUCTION

The center of avian life-history evolution has always been to comprehend the variation between key traits of species (Martin, 2004, 2015). Therefore, understanding why species have different life history traits is an essential question in the study of the evolution of life history (Partridge and Harvey, 1988). Traits of life history are related to reproduction, such as nest sites, egg color, clutch size, which can provide support for solving problems associated with assessment of population status and conservation (Martin, 2002). Moreover, basic data on reproductive ecology of species help to form and perfect general theories on patterns and processes of life history evolution (Lack, 1947; Ricklefs, 1977; Bennett and Owens, 2002; Covas, 2012).

Tengmalm's owl (*Aegolius funereus*), known as boreal owl in North America, traditionally inhabit conifer forests in boreal climatic zones of Eurasia and North America, showing a circumpolar distribution within the holarctic (Voous, 1962; Dementiev *et al*., 1970; König *et al*., 1999). However, recent studies have shown that boreal owls are also distributed in Southern European and southwestern states of the United States (Korpimäki and Hakkarainen, 2012). Boreal owls are nocturnal, dwelling in extensive coniferous forests in boreal and sub-alpine locations of the northern wood belt, but also mixed forests with old deciduous trees in lower altitudes. These owls strictly are dependent on old stands, as they nest exclusively in natural tree cavities, large woodpecker holes, or artificial nest-boxes as substitutes (Mikkola, 1983; König and Weick, 2008). Main prey are small mammals (such as

* Corresponding author: sunyh@ioz.ac.cn
0030-9923/2024/0002-0533 $ 9.00/0

voles, mice, lemmings and shrews), but birds and insects in lower portions also (Klaus *et al*., 1975; Cramp, 1977; Korpimäki, 1981).

Traditionally six subspecies of *A. funereus* are accepted in Eurasia; *A. f. funereus* is distributed in continental Europe and Northern Europe; *A. f. magnus* is distributed in Northeast Siberia and Kamchatka Peninsula; *A. f. sibiricus* is distributed in Central Siberia to Sakhalin Island and Northeast China; *A. f. pallens* is distributed in Siberia east to northern Mongolia; *A. f. caucasicus* is distributed in Caucasus and Crimea, and *A. f. richardsoni* as seventh subspecies is distributed in North America (Del Hoyo *et al*., 1999). *A. f. beickianus* is distributed in coniferous forests of higher mountains, a rather narrow area in the Qinghai-Tibet Plateau, including Tianzhu County and Kangle County in Gansu Province; Guinan County in Qinghai Province; Jiuzhaigou County, Baoxing County and Yajiang County in Sichuan Province. In comparison to other subspecies, its range reaches relative higher elevations in more southern distribution (Stresemann, 1928; Zheng *et al*., 1991; Del Hoyo *et al*., 1999; Sun *et al*., 2004).

Breeding biology and behavioural ecology of boreal owl was intensively studied in Europe and North America, especially in Fenno-Scandia (Hörnfeldt *et al*., 1990; Hayward and Hayward, 1993b; Korpimäki and Hakkarainen, 2012). However, basic information on the *A. f. beickianus* in the conifer forests of the Qinghai-Tibet Plateau is still lacking, except sporadic reports about nest site and vocalization, since Stresemann (1928) first described this subspecies (Sun *et al*., 2004; Gu *et al*., 2006).

The geological uplift of the Qinghai-Tibet Plateau resulted in a complete separation of the alpine coniferous forests in the southeastern margin of the plateau from the northern taiga forest of Eurasia, which resulted in an evolutionary differentiation in sibling-species or sibling-subspecies. However, due to the persistence of a close genetic relationship, morphology and behavior of several species/ subspecies in Eurasia and North America maintained consistent characters. These phenomena are well documented f. i. in the studies on Sichuan jay (*Perisoreus internigrans*), which corresponds strikingly to Siberian jay (*P. infaustus*) and grey jay (*P. canadensis*); on Chinese grouse (*Tetrastes sewerzowi*) compared to hazel grouse (*T. bonasia*) and ruffed grouse (*Bonasa umbellus*), and Pere David´s Owl (*Strix davidi*) in relation to the Ural owl (*S. uralensis*) (Sun *et al*., 2001, 2015; Sun and Fang, 2010). From this aspect, the aim of this paper is to present data on the breeding ecology of boreal owl in the southeastern margin of the Qinghai-Tibet Plateau and to compare the parameters of reproduction with other subspecies. Conform with this goal we describe details of the breeding biology of *A. f. beickianus* in Gansu province (including clutch size, egg mass, length of incubation, nestling periods, breeding success, fledgling measurement), to carve out the specific characters of this subspecies at the Qinghai-Tibet Plateau.

MATERIALS AND METHODS

Study area

The study was conducted between April and August during the years 2003-2009 and 2017-2019 at Lian Hua Shan Natural Reserve which is situated in southern Gansu Province, central China (34°54′17″-35°01′43″N, 103°39′59″-103°50′26″ E, Fig. 1). The area of the reserve is about 12,000 ha, and the forest coverage rate of the reserve reaches 69.3%. This study was conducted in the core area which is about 3600 ha at the altitude of 2800 to 3200 m above sea level. The mean annual temperature of the reserve is 5.1℃ to 6.0℃, the highest monthly mean temperature occurs in July, reaching 21.1℃, followed by August and June, which is 20.8℃ and 19.7℃, respectively. The lowest average monthly temperature is in January which is -15.6℃, -12.9℃ in December and -11.9℃ in February, respectively. The mean annual precipitation is 621 mm, and most precipitation occurres in April, May and June, which accounts for 31.1% of the annual precipitation. It usually snows after September, and generally continues to between the end of April and early May in the next year. The slope ranges from 20° to 40°, and the type of vegetation differs due to exposition. On the northern, shady, and humid slopes the vegetation typically constists of coniferous trees (dominant species are *Abies fargesii* and *Picea asperata*), mixed by some deciduous trees (*Populus davidiana*, *Betula utilis*, *Salix* spp. etc.) and shrubs. The sunny and marked dryer slopes are dominated by grasses and thickets, mostly of Willows (*Salix* spp.), Berberis (*Berberis* spp.) and Sea Buckthorn (*Hippophae rhamnoides* ssp. *sinensis*) (Sun *et al*., 2008).

Breeding sites and field observations

A total of 67 nest-boxes had been installed on coniferous trees in spruce-fir forest of the study area in 2002 and 2003. All nest boxes were placed far away from the road and were about 5 meters above the ground. These boxes were made from darkened wood-board and mostly had a square bottom with the inner length of 20 cm. The diameter of entrance was 8 cm, about 50 cm above bottom. For nest-controls the roofs could be opened easily (Korpimäki, 1981, 1985; Scherzinger and Mebs, 2020).

An aluminum extension ladder and foot clasp were used to check the nest boxes. After the breeding season, the nest boxes were cleaned and then spread with about 5 cm of wood chips on the bottom. The broken boxes would be repaired or replaced. Play-back and recording of territorial song were used to facilitate field surveys and locate which nest boxes would be occupied. The acoustic presentation lasted for 1-2 min every 0.5 km, and was followed by listening for about 2 min (Holmberg, 1979). We also used infrared camera to monitor inside and outside of the nest box.

Data on the owls' breeding performance were collected by checking the boxes in late March, April and early May, but also in June, when some owls replaced a failed brood in the early breeding season (Korpimäki, 1981, 1987a). Boxes were checked as frequently as essential to identify laying date, clutch size, the hatching date of nestlings and the number of fledglings (Korpimäki, 1987a, b). We usually checked confirmed broods during 6:30-8:00 every other day. In some cases (such as rainy or snowy days), the interval was three or four days.

The activity nest box was defined as at least one egg was laid. Breeding success was defined by laying ≥ 1 egg and rearing ≥ 1 nestling (Korpimäki, 1981; 1987a). The breadth (*B*) and length (*L*) of eggs were measured by vernier calipers (mm, rounded to two decimal places). The egg volume was calculated by quote of $\pi \times L \times B^2/6000$ (Tatum, 1975; Hörnfeldt *et al*., 1990).

Due to the behavior of the female we divided the nestling period into two stages; stage 1: female in the breeding-hole, warming, feeding and protecting small nestlings; stage 2: female leaves the nestlings as soon as the young are able to maintain their body temperature and to feed deposited prey on their own (Korpimäki, 1981), stays outside the hole or starts a second clutch elsewhere. Banding and measuring of adult females and their nestlings occurred, when nestlings were two to three weeks old (Korpimäki, 1981; 1987b).

RESULTS

Basic data on reproduction

Within 10 years (2003-2009, 2017-2019) we detected 51 active broods, with an average of 5.1 ± 1.7 broods per year. 19 nest-sites were used only once, but some were used repeatedly (10 nests 2 times, 4 nests three times) (Fig. 1). Breeding data of *A. f. beickianus* was collected from 23 nest-boxes in the years of 2004, 2009, 2017, 2018, and 2019 from April to July, 12 broods were found in egg-laying period, 7 nests in incubation period, and 4 in nestling period.

Egg-laying was initiated from April to June and the breeding season ended in late July. The first egg and last egg recorded was laid on April 7th and June 6th, respectively. The laying date of boreal owl culminated in the second half of April and the first half of May (n = 12 broods).

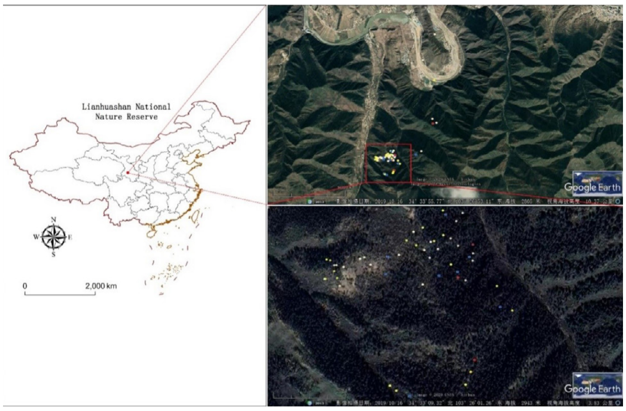

Fig. 1. The distribution of nest boxes for boreal owl at Lian Hua Shan. White for unused nests, yellow for breeding once, blue for breeding twice, red for breeding three times.

Fig. 2. The adult bird (A), egg (b, red arrow) and nestlings (B), 1 day old, (C) nestlings opened their eyes (12 days old), (D) The female left the nest-box (17-21 days old) (photographed by Yongke Zhu and Yun Fang).

A total of 60 eggs were registered in 23 nests, and 30 eggs of them were measured from 11 nests. The eggs are pure white (Fig. 2B, red arrow). The mean clutch size was 2.61 ± 0.64 (range: 2-4, n = 23 broods in 5 years), clutches mostly contented two and three eggs. The mean egg mass was 12.42 ± 1.36 g (range: 9.85-15.10 g, n = 30), the mean egg length and width were 33.44 ± 1.14 mm and 27.08 ± 0.67 mm (length range: 31.10-35.80 mm, n = 30; width range: 24.68-28.40 mm, n = 30), the egg volume was 12.85 ± 0.79mm^3 (range: 10.89-14.49 mm^3, n = 30)

(Table I). Consecutive eggs were laid in intervals of 2.5 ± 0.5 days (n = 5 broods).

Table I. Breeding parameters of *A. f. beickianus* at Lianhuashan.

Parameters	Mean±SD	N
Egg		
Length (mm)	33.44 ± 1.14	30
Width (mm)	27.08 ± 0.67	30
Weight (g)	12.42 ± 1.36	30
Volume (mm^3)	12.85±0.79	30
Clutch size	2.61±0.64	23
Incubation time (d)	29.8±1.22	15
Nestling period		
1 (d)	16.75±1.48	4
2 (d)	17±4.34	5
Total (d)	35.75±2.8	12
No. of fledglings[a]	2.07±0.38	13
No. of fledglings[b]	1.25±0.31	23
Nestling weight (g)	112.03 ± 9.79	17

[a]per nesting attempt. [b]per successful brood. The d is day and the g is gram.

Incubation and nestling period

Incubation time was 29.8 ± 1.22 days (range: 27-31 days, n = 15 eggs in 8 broods). It was recorded by camera that female brooded alone and was fed by male during the incubation period, and prey was delivered at the entrance of the nest-box (n = 1 nest, Table I).

The chicks hatched one by one. Freshly hatched nestlings were covered with short white downs of the neoptile, eyes were closed and the young still unable to raise their head or stand on feet (Fig. 2B, blue arrow). Eyes open about the 12th day (Fig. 2C). The blackish brown feathers of the mesoptile, typic for the later nestling period, gradually replaced the white down at wings, head, and back. There was no sanitary in the nest, so the nestlings were raised in a stinking layer of rotten food scraps, pellets and feces. The nestling period took 35.75 ± 2.80 days in total (range: 31-43, n = 12 nests, Table I). The first stage, when the female was in the nesting hole, lasted 16.75 ± 1.48 days (range: 15-19, n = 4 nests, Table I). The second stage, when the female stood outside the nest until the young left the nest, lasted 17 ± 4.34 days (range: 11-22, n = 5 nests, Table I). The mean interval days between each fledgling leaving the nest was 2.55 ± 1.92 days (n = 19 nestlings in 8 nests). The mean weight of nestlings before fledging was 112.03 ± 9.79 g (n = 17 nestlings in 9 nests, Table I).

At the end of nestling period, when the young owls were about 4 weeks old, the fledglings typically looked dark chocolate-brown with a black facial disc, significant whitish eyebrows, a few white spots on their wings, and some washy vertical stripes in milky white on the lower breast and belly (Fig. 2D).

Breeding success

Overall 41 nestlings hatched in 23 broods (n = 60 eggs), 19 eggs did not hatch, among those 16 eggs were abandoned, 2 eggs were unfertile and one lost. The mean number of young hatched was 1.76 ± 0.33 per nesting attempt (n = 23 broods in 5 years). The hatching success reached 70.85 % ± 10.38 % (n = 23 broods in 5 years). The reproductive success was 56.5% which produced at least one nestling from 23 initiated broods (n = 13 broods). During the five-year period, 27 nestlings fledged successfully, 14 nestlings failed before fledging, among those 8 nestlings were dead, 5 nestlings stolen by human and one nestling predated by a leopard cat (*Prionailurus bengalensis*) recorded by automatic video. The mean number of fledglings was 1.25 ± 0.31 (n = 23 broods, Table I) per nesting attempt. The number of fledglings in successful nesting varied from 1 to 4, averaged 2.07 ± 0.38 (n = 13 broods, Table I).

DISCUSSION

In this study we present basic information on the breeding biology, including clutch size, duration of incubation, and reproductive success of the boreal owl (*A. f. beickianus*) in the mountainous forests of Gansu. Within 10 years of survey we found 23 initiated broods. The eggs are pure and pale white without speckles, the incubation and nestling periods were 29.8 and 35.75 days each. In respect to the fledgling rate, the hatching success was 70.85% and the reproductive success was 56.5%, respectively.

In our study area egg-laying started in early April, with a peak in the middle of April (range 7th April - 6th June). Regarding the average date, start of egg-laying in the high mountains could be characterized by a delay of up to 2 weeks, when compared to conditions in Central Europe (f. i. Germany and Czech Republic: end of March to beginning of April (Zarybnicka and Vojar, 2013; Kouba *et al*., 2015; Scherzinger and Mebs, 2020), Northern Italy: first week of April (Mezzaville and Lombardo, 2013), Fenno-Scandia: middle of March to early May (Hörnfeldt and Eklund, 1990; Korpimäki and Hakkarainen, 2012). Due to the huge area of distribution of the American boreal owl, covering different latitudes and sea levels, the egg-laying of *A. f. richardsoni* shows a broad amplitude. An extensive breeding area from Colorado to Alaska: f. i. 6th of March till 6th of June in Alberta (mean date = 22nd of March; Priestley, 2008); end of March in Montana, Minnesota and Alaska (Hayward, 1994; Duncan and Lane, 1987), middle to end of April in the Rocky Mountains and NW-Alberta (Hayward *et al*., 1993b; Domahidi *et al*., 2020). Further dates for egg-laying in mean are May 1st in Idaho, May 10th in Colorado, middle of May in Nova Scotia (Ryder *et al*., 1987; Duncan and Lane, 1987; Hayward *et al*., 1993b; Hayward, 1994; Lauff, 2009; Domahidi *et al*., 2020).

Korpimäki (1981) argued that the reproductive activity of the owls follows the periodic fluctuations of Microtus voles, by influencing mating-systems, egg-laying, clutch size and the density of populations. In "mouse-years" egg-laying may start in late February (f. i. Germany; Meyer, 2006; Kämpfer-Lauenstein and Lederer, 2010), compared to end of May or even middle to end of June in years with poor availability of prey (Zarybnicka, 2009; Ravussin *et al*., 2015; Kouba *et al*., 2017). In our study area, the average altitude is around 2,800m, thus snow could cover the ground layer in March, and even till the beginning of April, what may lead to a shortage of food in early spring time and a delay of the birds' breeding.

Comparing the size and volume of the eggs from European and North American subspecies, we found that the eggs of *A. f. beickianus* in the Lian Hua Shan are somewhat larger: f. i. mean measure 33.44 x 27.08 mm in *A. f. beickianus* from Gansu, compared to 31.5 x 26.3 mm in *A. f. funereus* from Italy (n = 569 eggs; Mezzaville and Lombardo, 2013), 32.7 x 26.6 mm from Germany (n = 128 eggs), 33.3 x 27.2 mm from Sweden (n = 148 eggs; Glutz von Blotzheim and Bauer, 1980), very few measures exist from the American subspecies: 32.2 x 26.9 mm in mean (range for length 29.0-36.6 mm, for width 25.4-28.8 mm; n = 49 eggs (Bent, 1938; Hayward and Hayward, 1993). Analogous the egg-volume was 12.85 mm^3 (range 10.9-14.5 mm3), compared to 11.58 mm^3 (range 7.8-14.2 cm^3) in eggs from Northern Italy (n = 569; Mezzaville and Lombardo, 2013), and 11.6-12.5 mm^3 in eggs from Finland (n = 268; Hakkarainen and Korpimäki, 1994; Scherzinger and Mebs, 2020).

The mean clutch size in Lian Hua Shan was 2.61 eggs (range 2-4), which was lower than that in Europe, f. i. 3.2 eggs in Italy (n = 93 clutches; Mezzaville and Lombardo, 2013), 4.7 in northern Germany (maximal 10 eggs per clutch; n = 85 clutches; Schwerdtfeger, 1984), 5.3 eggs in Switzerland (maximal 9 eggs; n = 440 clutches; Ravussin *et al*., 2015), 5.4 eggs in western Germany (maximal 10 eggs in years of seed-mast; n = 80 clutches; Kämpfer-Lauenstein and Lederer, 2010), 6.6 eggs in Czech Republic (n = 70 clutches; Zarybnicka and Vojar, 2013), 5.65 eggs in Sweden (n = 109 clutches; Hörnfeldt *et al*., 1990), 5.6 eggs in Finland (n = 412 clutches; Korpimäki, 1987b) (Table II). Clutches in the American subspecies *A. f. richardsoni* are remarkably small also: 2.5 eggs in 4 broods, respectively 3.75 eggs in 8 broods (range 2-6 eggs) in Alberta (Domahidi, 2018, 2020); 2.5-3.5 eggs in Idaho (Hayward, 1994); 2-4 eggs in Colorado (Ryder *et al*., 1987); 3-4 eggs in Nova Scotia (Lauff, 2009); and 2-6 eggs in Montana (Montana Field Guide) (Table II).

No doubt, clutch size is a key-factor in the trajectory of life-history (Stearns, 1976, 1977; Ricklefs, 1977; Bell, 1980). Lack (1947) argued that the number of eggs in the clutch was in relation to the mean number of young birds, which parents can feed and rear. In this model the key factor is the amount of food available during the period of rearing nestlings and fledglings (Lack, 1948, 1954). An opposite view suggests that the key factor is the amount of food, the females can get during the period of egg-production, so the number of laid eggs remains below the number of fledglings that parents could feed potentially (Perrins, 1970; Haartman, 1971). In this study, 8 dead nestlings were found before fledging, which may be caused for the shortage of food resources in the late brooding period. We also found that mean weight of nestlings before fledging (112.03 ± 9.79 g) was less than that of Finland (122.2g) (Korpimäki, 1981), thus we believe that clutch size was lower in our study which may be explained by Lack's idea that the number of eggs caused by the brooding period food resources.

In the forests of Lian Hua Shan the time of brooding lasted from the second half of April to the first half of May. In this landscape, the mean incubation period lasts 29.8 ± 1.22 days (range 27-31 days; n = 15 nests), which differs only insignificant from European conditions and American (f. i. 27-30 days in Germany (Scherzinger and Mebs, 2020)). In a Finnish study Korpimäki and Hakkarainen (2012) found, that the youngest nestling hatched after 26.6 days of incubation, compared to the eldest sibling with 29.2 days (Table II). In full accordance, brooding in the American Boreal Owl lasts 26-32 days in all (Hayward and Hayward, 1993); referred to regional conditions 28-29 days in Montana (Montana Field Guide), and 29-34 days in Alberta (Priestley, 2008) (Table II).

The first stage of the nestling period (when the female still covered its nestlings), in Lian Hua Shan took only 16.75 days (range 15-19 days), compared to more than 21 days under European conditions (f. i. 3 weeks in Czech Republic (Kouba *et al*., 2015), and 22.2 to 24.8 days after hatching of 1st nestling ibidem, dependent on prey abundance (Zarybnicka, 2009), following by 21.4 days in Finland (Zarybnicka and Vojar, 2013), and even 25 days in average in Norway (range 17-31 days, dependent on number of nestlingsnestlings; Eldgard and Sonerud, 2012). In the American subspecies this phase lasts 17-22 days.

Table II. Breeding parameters of boreal owls in various study areas of Asia, Europe and North America

Study area	Clutch size	Incubation time	Nestling period 1	Nestling period total	No. of fledglings[a]	No. of fledglings[b]	Source
China (Lian Hua Shan)	2.61±0.64	29.8±1.22	16.75±1.48	35.75±2.8	1.25±0.31	2.07±0.38	1
Fenno-candia (Finland)	5.7-5.8	26.6-29.2	21.4- 25	30.3- 32.6	3.0	3.9	2, 3, 4, 5, 6
Fenno-candia (Sweden)	5.6		—	—	—	—	7
Norway	—	—	25	—	—	—	8
Italy	3.2	—	—	—	—	2.7	9, 10
Switzerland	5.3	—	—	—	—	3.15	11
Germany (Northern region)	4.7	27-30	—	32.4	—	4.5	12,13, 14
Germany (Arnsberger Wald)	5.4	—	—	—	—	4.2	15
Germany (Munich)	—	—	—	—	—	3.2-5.2	16
Czech Republic	6.6	—	22.2-24.8	31.5-34.2	0.7-3.9	2.0-5.9	17, 18, 19, 20
Canada (Alberta)	2.5; 2.75	29-34	—	—	0.5	—	21, 22
Canada (Nova Scotia)	3.2	—	—	—	2.25	—	23
America (Idaho)	2.5-3.5	26-32	17-22	27-32	2.3	—	24, 25, 26
America (Montana)	2-6	28-29	—	—	—	—	27
America (Colorado)	2-4	—	—	—	—	—	28

[a]per nesting attempt. [b]per successful brood. Source: (1) Data of Lianhuashan, (2) Zarybnicka and Vojar 2013, (3) Eldgard and Sonerud 2012, (4) Korpimäki 1987c, (5) Zarybnicka *et al*. 2012, (6) Korpimäki and Hakkarainen 2012, (7) Hörnfeldt and Eklund 1990b, (8) Eldgard and Sonerud 2012, (9) Mezzaville and Lombardo 2012, (10) Mezzavilla *et al*. 1994, (11) Ravussin *et al*. 2015, (12) Schwerdtfeger 1984, 2014, (13) Scherzinger and Mebs 2020, (14) Kuhk 1969, (15) Kämpfer-Lauenstein and Lederer 2010, (16) Meyer 2006, (17) Zarybnicka and Vojar 2013, (18) Kouba *et al*. 2014, 2015, (19) Zarybnicka 2009, (20) Kouba *et al*. 2017, (21) Domahidi 2018, 2020, (22) Priestley 2008, (23) Lauff 2009, (24) Hayward 1994, (25) Hayward and Hayward 1993, (26) Hayward *et al*. 1993, (27) Montana Field Guide, (28) Ryder *et al*. 1987.

(Hayward *et al*., 1993) (Table II). It may be due to the smaller clutches in this study as the female warmed fewer nestlings and invested less time in temperature control in the nesting-hole which caused the first stage shorter.

The mean time of whole the nestling period lasted 35.75 days (range 31-43 days) in Lian Hua Shan, and therefore was slightly longer than in European subspecies. The duration of this period was recorded by automatic cameras in Finland and in the Czech Republic as well, and lasted 31.5-34.2 days in average (extremes 27-38 days; Kouba *et al*., 2014, 2015); the average duration for Germany is 32.4 days (range 29-36 days; Kuhk, 1969; Scherzinger and Mebs, 2020). In a Finnish study fledging occurred at an age of 30.3 days in the youngest nestling, but 32.6 days in the oldest one (Korpimäki and Hakkarainen, 2012). In North-American Boreal Owls the nestling period lasts for 27 to 32, sometimes 36 days (Hayward and Hayward, 1993; Hayward *et al*., 1993) (Table II). As mentioned before, the first stage of nestling was shorter, however, the whole nestling period was slightly longer, which may be caused by insufficient food in the second stage of nestling so that parents would invest more time on feeding the nestlings for leaving the nesting-site with target-weight. In another study we found that there was a nestling dead due to food shortage based on the camera record in the late brooding period (unpublished data).

This is highly consistent with the concerning low number of eggs, hatchlings and fledglings in this area, probably caused mainly by shortage of food: Percentage of successful hatching was 70.85 % in Lian Hua Shan, compared to 86.8 % in boreal owl of northern Italy (Mezzavilla *et al*., 1994) and 52.7-100 % in Czech Republic depending on prey availability (Zarybnicka, 2009). While Chinese broods contained 1.76 hatchlings only (n = 23 nests), German broods had 2.6 to 4.2 nestlings per initiated brood (Meyer and Melle, 2010; Kämpfer-Lauenstein and Lederer, 2010), Czech broods 4.4 nestlings on an average, but Finnish broods 6.0 nestlings (Korpimäki and Hakkarainen, 2012; Zarybnicka *et al*., 2012).

Such differences correlate with the number of successful fledglings also, reaching 1.25 fledglings per initiated brood, and 2.07 fledglings per successful nest. The reproductive success was 56.5%. In peak-years of small mammals, the success of reproduction reached 81% in Germany, what corresponds with 4.5 fledglings per successful nest (Schwerdtfeger, 1984; Schwerdtfeger and Wink, 2014), and 3.2-5.2 in Munich (Meyer, 2006), 4.2 in Arnsberger Wald (Kämpfer-Lauenstein and Lederer, 2010). It reached 2.7 in northern Italy (Mezzavilla *et al*., 1994), 3.15 in Switzerland (Ravussin *et al*., 2015), 3.9 in Finland

(Korpimäki, 1987b). But under a mountainous climate in the Czech Republic the breeding success also was rather meager, with 37 till 45.5 % per initiated brood (Zarybnicka and Vojar, 2013), resulting in 0.7-3.9 fledglings per initiated brood, and 2.0-5.9 per successful brood (Kouba *et al*., 2017) (Table II). In the American Boreal owl breeding success reaches rather low numbers also, with a mean of 0.5 fledglings in NW-Alberta (Domahidi, 2018; Domahidi *et al*., 2020), 2.25 in Nova Scotia (Lauff, 2009) and 2.3 fledglings in Idaho (Hayward, 1994) (Table II).

By comparing the difference in the breeding ecology of boreal owl from Central Asia to Europe and North America, we point to the extreme environmental conditions in high altitudes, with long-lasting snow-cover, rainy periods in the breeding season and poor ground vegetation under a closed canopy, which may limit the availability of small mammals. To clarify this aspect, further studies on food composition and richness are required.

CONCLUSIONS

In this study, we presented the breeding information of the subspecies of boreal owl (*A. f. beickianus*), including egg-laying date, clutch size, egg size, incubation period, nestling period, nestling fate, reproductive success rate, which would be helpful for further study about population and conservation of this subspecies.

ACKNOWLEDGMENTS

This study was supported by the National Natural Science Foundation of China (No. 31520103903 and 32011530077) and BP Conservation Programme. We thank Yingxin Jiang, Jinlin Li, Yongqi Yang and Yongsheng for their help of field work and the staffs of Lian Hua Shan Nature Reserve for their support at any time.

Statement of conflict of interest

The authors have declared no conflict of interest.

REFERENCES

Bell, G., 1980. The costs of reproduction and their consequences. *Am. Nat.,* **116**: 45-76. https://doi.org/10.1086/283611

Bennett, P.M. and Owens, I.P.F., 2002. *Evolutionary ecology of birds: Life histories, mating systems and extinction*. Oxford University Press, Oxford.

Bent, A.C., 1938. *Life histories of North American birds of prey,* pt. 2: Orders Falconiformes and Strigiformes. Bulletin of the United States National Museum. pp. 92.

Cramp, S., 1977. *Handbook of the birds of Europe, the Middle East, and North Africa: The birds of the western Palearctic*. Oxford University Press, Oxford, UK, pp. 960.

Covas, R., 2012. Evolution of reproductive life histories in island birds worldwide. *Proc. Roy. Soc B-Biol. Sci*., **279**: 1531-1537. https://doi.org/10.1098/rspb.2011.1785

Del Hoyo, J., Elliott, A. and Sargatal. J., 1999. *Handbook of the birds of the world. Barn-owls to hummingbirds*. Lynx Edicions, pp. 156.

Dementiev, G.P., Gladkov, N.A. and Blagosklonov, K.N., 1970. *Birds of the Soviet Union. vol. I. Israel program for scientific translations*. Smithsonian Inst., Washington, DC.

Domahidi, Z., 2018. *Distribution and breeding ecology of Boreal and Northern Saw-whet owls in the boreal forest of Alberta, Canada*. MSc. thesis Univ. Alberta, **81**. https://doi.org/10.5751/ACE-01445-140214

Domahidi, Z., Nielsen, S., Bayne, E. and Spencer, J., 2020. Boreal owl (*Aegolius funereus*) and Northern Saw-whet owl (*Aegolius acadicus*) breeding records in managed forest. *Can. Field Natl. List*, **134/2**: 125-131. https://doi.org/10.22621/cfn.v134i2.2146

Duncan, J. and Lane, P., 1987. Breeding boreal owls in Roseau county. *Loon*, **59/4**: 163-164.

Eldegard, K. and Sonerud, G.A., 2012. Sex roles during post-fledgling care in birds: female Tengmalm´s owl contribute little to food provisioning. *J. Ornithol.,* **153**: 385-398.

Gu, Y., Fang, Y. and Sun, Y.H., 2006. Vocalization of boreal owl (*Aegolius funereus beickianus*) in breeding season in Lianhuashan, Gansu Province. *Sichuan J. Zool.*, **25**: 1. (Translated from the Chinese).

Glutz von Blotzheim, U.N. and Bauer, K.M., 1980. *Handbuch der Vögel Mitteleuropas*. Akademische Verlagsgesellschaft, Wiesbaden, Germany.

Haartman, L.V., 1971. Population dynamics. In: *Avian biology* (eds. D. Farner and J.R. King). Academic Press, New York, pp. 391-459.

Hakkarainen, H. and Korpimäki, E., 1994. Environmental, parental and adaptive variation in egg size of Tengmalm's owls under fluctuating food conditions. *Oecologia*, **98**: 362-368. https://doi.org/10.1007/BF00324225

Hayward, G.D. and Hayward, P.H., 1993a. Boreal owl (*Aegolius funereus*). *Birds North Am.*, **63**: 1-19. https://birdsna.org/Species-Account/bna/species/borowl/introduction, https://doi.org/10.2173/tbna.63.p

Hayward, G.D., Hayward, P.H. and Garton, E.O., 1993b. Ecology of boreal owls in the northern

Rocky Mountains, USA. *Wildl. Monogr.*, **124**: 3-59. https://doi.org/10.1007/BF00324225

Hayward, G.D., 1994. Review of technical knowledge: Boreal owl. In: *Flammulated, boreal, and great gray owls in the United States. USDA Techn. Rep. RM-253*, **9**: 92-127. https://doi.org/10.2737/RM-GTR-253

Holmberg, T., 1979. Point transect census of Tengmalm's Owl-a methodological study. *Var Fagelvarld*, **38**: 237-244.

Hörnfeldt, B., Carlsson, B.G., Löfgren, O. and Eklund, U., 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). *Can. J. Zool.*, **68**: 522-530. https://doi.org/10.1139/z90-077

Hörnfeldt, B. and Eklund, U., 1990. The effect of food on laying date and clutch-size in Tengmalm's Owl *Aegolius funereus*. *Ibis*, **132**: 395-406. https://doi.org/10.1111/j.1474-919X.1990.tb01058.x

Kämpfer-Lauenstein, A. and Lederer, W., 2010. Populationsdynamik des Rauhfußkauzes *Aegolius funereus* im Arnsberger Wald. *Charadrius*, **42**: 69-78. http://www.nw-ornithologen.de/images/textfiles/charadrius/charadrius46_1_2_69_78_kaempferlauenstein_lederer_raufusskauz.pdf

Klaus, S., Mikkola, H. and Wiesner, J., 1975. Aktivität und Ernährung des Rauhfußkauzes *Aegolius funereus* (L.) während der Fortpflanzungsperiode. *Zool. Jb. Syst.*, **102**: 485-507.

König, C. and Weick, F., 2008. *Owls of the world*. Christopher Helm, London, United Kingdom, pp. 441-444.

König, C., Weick, F. and Becking, J.H., 1999. *Owls: A guide to the owls of the world*. Pica Press, 392-395.

Korpimäki, E., 1981. On the ecology and biology of Tengmalm's owl *Aegolius funereus* in Southern Ostrobothnia and Soumenselka, western Finland. *Acta Univ. Oul. A. Sci. Rer. Nat.*, **118**: 1-84.

Korpimäki, E., 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus*. *Ecography*, **8**: 175-180. https://doi.org/10.1111/j.1600-0587.1985.tb01168.x

Korpimäki, E., 1987a. Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. *Ibis*, **129**: 58-68. https://doi.org/10.1111/j.1474-919X.1987.tb03159.x

Korpimäki, E., 1987b. Clutch size, breeding success and brood size experiments in Tengmalm's owl *Aegolius funereus*: A test of hypotheses. *Ornis Scand.*, **18**: 277-284. https://doi.org/10.2307/3676896

Korpimäki, E. and Hakkarainen, H., 2012. *The Boreal owl: Ecology, behaviour and conservation of a forest-dwelling predator*. Cambridge University Press, pp. 17. https://doi.org/10.1017/CBO9780511844164

Kouba, M., Bartos, L. and Zarybnicka, M., 2014. Perching of Tengmalm´s Owl (*Aegolius funereus*) nestlings at the nest box entrance: effect of time of the day, age, wing length and body weight. *PLoS One*, **9**: e97504. https://doi.org/10.1371/journal.pone.0097504

Kouba, M., Bartos, L., Korpimäki, E. and Zarybnicka, M., 2015. Factors affecting the duration of nestling period and fledging order in Tengmalm´s Owl (*Aegolius funereus*): Effect of wing length and hatching sequence. *PLoS One*, **9**: e67034. https://doi.org/10.1371/journal.pone.0121641

Kouba, M., Bartos, L., Sindelar, J. and Staastny, K., 2017. Allpoparental care and adoption in Tengmalm´s owl (*Aegolius funereus*). *J. Ornithol.*, **158**: 185-191. https://doi.org/10.1007/s10336-016-1381-z

Kuhk, R., 1969. Schlüpfen und Entwicklung der Nestjungen beim Rauhfußkauz (*Aegolius funereus*). *Bonn. Zool. Beitr.*, **20**: 145-150.

Lack, D., 1947. The significance of clutch-size. *Ibis*, **89**: 302-352. https://doi.org/10.1111/j.1474-919X.1947.tb04155.x

Lack, D., 1948. The significance of clutch-size. Part III. Some interspecific comparisons. *Ibis*, **90**: 25-45. https://doi.org/10.1111/j.1474-919X.1948.tb01399.x

Lack, D., 1954. *The natural regulation of animal numbers*. Oxford University Press, London.

Lauff, R.F., 2009. First nest records of the boreal owl *Aegolius funereus* in Nova Scotia, Canada. *Ardea*, **97**: 497-502. https://doi.org/10.5253/078.097.0414

Martin, T.E., 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proc. Roy. Soc. B Biol. Sci.*, **269**: 309-316. https://doi.org/10.1098/rspb.2001.1879

Martin, T.E., 2004. Avian life-history evolution has an eminent past: Does it have a bright future? *Auk*, **121**: 289-301. https://doi.org/10.1093/auk/121.2.289

Martin, T.E., 2015. Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science*, **349**: 966-970. https://doi.org/10.1126/science.aad1173

Meyer, H., 2006. Ein Spitzenjahr des Rauhfußkauzes *Aegolius funereus* auf der Münchner Schotterebene. *Anzeiger*, **45**: 55-61.

Meyer, W. and Melle, M., 2010. Mehr als drei Jahrzehnte Untersuchungen am Rauhfußkauz *Aegolius funereus* Beobachtungen bei der praktischen Arbeit. *Berichte Vogelwarte Hiddensee*, **20**: 75-82.

Mezzavilla, F., Lombardo, S. and Sperti, M.T., 1994. *First data on biology and breeding success of Tengmalm´s owl* Aegolius funereus *in Cansiglio*. *Mus. Reg. Sci. Nat. Turinol*., pp. 325-334.

Mezzaville, F. and Lombardo, S., 2013. Indagini sulla biologia riproduttiva della civetta capogrosso Ageolius Funereus: ANNI 1987-2012. In: Atti Secondo Convegno Italiano Rapaci Diurni e Notturni (eds., F. Mezzavilla and F. Scarton). Treviso, 12-13 ottobre 2012. Associazione Faunisti Veneti, Quaderni Faunistici n. 3: 312.

Mikkola, H., 1983. *Owls of Europe*. T and AD Poyser. Calton, UK, pp. 397.

Montana Field Guide, 2011. *Boreal owl* Aegolius funereus. https://fieldguide.mt.gov/speciesDetail.aspx?elcode=ABNSB15010

Partridge, L. and Harvey, P.H., 1988. The ecological context of life history evolution. *Science*, **241**: 1449-1455. https://doi.org/10.1126/science.241.4872.1449

Perrins, C.M., 1970. The timing of birds' breeding seasons. *Ibis*, **112**: 242-255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Priestley, L., 2008. The nesting phenology of Northern Saw-whet Owl and Boreal Owl in Central Alberta. *Nat. Alberta*, **38**: 20-25.

Ravussin, P.A., Trollet, D., Daenzer, C., Longchamp, L., Romailler, K. and Metraux, V., 2015. Quel avenir pour la Chouette de Tengmalm *Aegolius funereus* dans le massiv du Jura. Bilan de trente annees de suivi. *Nos Oiseaux*, **62**: 5-28.

Ricklefs, R.E., 1977. On the evolution of reproductive strategies in birds: Reproductive effort. *Am. Nat*., **111**: 453-478. https://doi.org/10.1086/283179

Ryder, R., Palmer, D. and Rawinski, J., 1987. Distribution and status of the Boreal Owl in Colorado. In: *Biology and conservation of northern forest owls: symposium proceedings. U. S. For. Ser. Gen. Tech. Rep*., **RM-142**: 169-174. https://xs.dailyheadlines.cc/books?hl=zh-CNandlr=andid=FzZHAAAAYAAJandoi=fndandpg=PA169andots=Aj8uRxBfJ7andsig=yOGJF-INtQVDjmfSq_0zKpKisQg

Schwerdtfeger, O., 1984. Verhalten und Populationsentwicklung des Rauhfußkauzes (*Aegolius funereus*). *Vogelwarte*, **32**: 183-200.

Schwerdtfeger, O. and Wink, M., 2014. Lack of correlation between sex ratio and food supply or other biotic variables in nestlings of Tengmalm´s Owl *Aegolius funereus*. *J. Ornithol*., **155**: 497-505. https://doi.org/10.1007/s10336-013-1032-6

Scherzinger, W. and Mebs, T., 2020. *Die Eulen Europas (Owls of Europe).* Franckh-Kosmos Verlags, Stuttgart, Deutschland. (in German).

Stearns, S.C., 1976. Life-history tactics: A review of the ideas. *Q. Rev. Biol*., **51**: 3-47. https://doi.org/10.1086/409052

Stearns, S.C., 1977. The evolution of life history traits: A critique of the theory and a review of the data. *Annu. Rev. Ecol. Systemat*., **8**: 145-171. https://doi.org/10.1146/annurev.es.08.110177.001045

Stresemann, E., 1928. *Aegolius funereus beickianus*. *Orn. Monatsb*., **36**: 41.

Sun, Y.H., Scherzinger, W., Liu, N., Klaus, S. and Fang, Y., 2001. The new distribution areas of Sichuan wood owl (*Strix davidi*) in Gansu, China. *Acta Zool. Sin*., **47**: 473-475. https://doi.org/10.1046/j.1439-0361.2000.00053.x

Sun, Y.H., Fang, Y., Scherzinger, W. and Klaus, S., 2004. Breeding notes of the boreal owl (*Aegolius funereus beickianus*) at Lianhuashan in Gansu, China. *Chinese J. Zool*., **39**: 99-100. (Translated from the Chinese).

Sun, Y.H., Fang, Y., Klaus, S., Martens, J., Scherzinger, W. and Swenson, J.E., 2008. *Nature of the Lianhuashan natural reserve*. Liaoning Science and Techonology, Shenyang.

Sun, Y.H. and Fang, Y., 2010. Chinese grouse (*Bonasa sewerzowi*): its natural history, behavior and conservation. *Chinese Birds*, **1**: 215-220. https://doi.org/10.5122/cbirds.2010.0015

Sun, Y.H., Jia, C.X. and Fang, Y., 2015. The distribution and status of Sichuan grey jay (*Perisoreus internigrans*). *J. Ornithol*., **142**: 93-98. https://doi.org/10.1046/j.1439-0361.2000.00053.x

Tatum, J.B., 1975. Egg volume. *Auk*, **92**: 576-580. https://doi.org/10.2307/4084611

Voous, K.H., 1962. *Vogelwelt Europas und ihre Verbreitung*. Paul Parey, Hamburg.

Zarybnicka, M., 2009. Parental investment of female Tengmalm's owls, *Aegolius funereus*: Correlation with varying food abundance and reproductive success. *Acta Ornithol*., **44**: 81-88. https://doi.org/10.3161/000164509X464911

Zarybnicka, M., Korpimäki, E. and Griesser, M., 2012. Dark or short nights: Differential latitudinal constraints in nestling provisioning patterns of a nocturnally hunting bird species. *PLoS One*, **7**: e36932. https://doi.org/10.1371/journal.pone.0036932

Zarybnicka, M. and Vojar, J., 2013. Effect of male provisioning on the parental behavior of female boreal owls *Aegolius funereus*. *Zool. Stud*., **52**: 1-8. https://doi.org/10.1186/1810-522X-52-36

Zheng, Z.X., Xian, Y.H. and Guan, G.X., 1991. *Fauna sinica-Aves*. Vol.6. Science Press, Beijing. pp. 141-225 (Translated from the Chinese).