ORNIS SVECICA 24:41–50, 2014 https://doi.org/10.34080/os.v24.22563

Breeding biology of a Tawny Owl *Strix aluco* population in south-western Sweden – a 15 year survey

Häckningsbiologin hos en population av kattuggla Strix aluco *i sydvästra Sverige – en femtonårig studie*

PETER ERICSSON, LARS-OVE NILSSON, KENT HAGLUND & DANIEL ERICSSON

Abstract

The breeding biology of the Tawny Owl *Strix aluco* was studied during 15 years in a 1000 km^2 area in south-western Sweden. The owls were breeding in c. 170 nest boxes, one in each of a potential territory. Occupancy rose from less than 20% in the first years to better than 50% in most of the later years. During the first years most nest boxes were relocated to sites within the territories that we considered to be of better quality. Absence of any increase in 48 high quality control territories indicates that the relocations were important for increasing population size. Nesting success was positively correlated with population density. This unexpected result could regrettably not be analyzed in relation to food abundance as we estimated food abundance by the number of prey found in nests. Bank vole, field vole and wood mice were the most predominant prey. All these three taxa had a peak in 2010 when owl density also peaked. The mean brood size was 2.3 young, similar to that in other European populations

Peter Ericsson, Sågvägen 24, 54395 Fagersanna, Sweden. Email: strix.ericsson@gmail.com (corresponding author)
Lars-Ove Nilsson, Lingonstigen 14B, 546 33 Karlsborg, Sweden
Kent Haglund, Gräshult, Hagalund, 546 91 Karlsborg, Sweden
Daniel Ericsson, Björkhult 7, 54395 Fagersanna, Sweden

Received 30 September 2013, Accepted 7 April 2014, Editor: S. Svensson

Introduction

There is a considerable interest of how reproductive success varies between years and over longer periods of time. A large number of articles have been written on the subject (for example, Lundberg 1976, Lundberg 1981, Tjernberg 1983). The interest focuses primarily on how to understand the mechanisms that regulate the size of animal populations. In many bird populations a correlation between food availability and reproductive success has been found. In particular, this applies to the impact of prey abundance on the reproductive output in top predators like raptors and owls (Newton 1979, Tjernberg 1983, Lundberg & Westman 1984, Wendland 1984, Hörnfeldt et al. 1990, Village 1990, Brommer et al. 1998, Rosenberg et al. 2003).

Tawny Owls *Strix aluco* feed on different kinds of animal prey but predominantly on small rodents, and the breeding density varies between years depending on prey abundance (Southern 1954, Mikkola 1983, Wendland 1984, Kirk 1992, Zalewski 1994). Hence, during rodent peak years in the breeding area, the owls often breed in large numbers (Southern 1954, 1970, Wallin 1988, Redpath 1995, Coles & Petty 1997, Petty & Fawkes 1997, Sunde 2001, Sunde et al. 2001, Persson 2003, Sunde et al. 2003, Avotins 2004, Kekkonen et al. 2008). In Wytham Wood at Oxford, Great Britain, a long-term study (1947–1959; Southern 1970) showed a mean value of 1.96 produced young per brood (n=76). Studies of Tawny Owls in two other forests in Great Britain showed that 84–96 percent of the population began to breed when food abundance was high, but only 30 percent when food abundance was low (Petty, 1987, Petty & Fawkes 1997).

The predominant prey species varies between different geographical areas. Studies of Tawny Owl diet from the British Isles showed that the most common prey was bank vole *Clethrionomys glareolus* and wood mouse *Apodemus sylvaticus* (Southern 1954, Kirk 1992). Another study in an upland forest showed that the most common prey was field vole *Microtus agrestis* (Petty 1987). When rodent abundance drops, Tawny Owls are able to change to alternative prey such as birds and amphibians but also beetles and earthworms (Mikkola 1983, König & Weick 2008).

The male is responsible for food delivery when the female incubates the eggs and until the young are about six days old (Mikkola 1983, König & Weick 2008, own observations). When food is abundant, the male sometimes loads up a stock of rodents in the nestbox (own observations).

The Tawny Owl is a common bird, perhaps the most common owl species in Europe (König & Weick 2008). It is non-migratory and strongly territorial. Immature birds usually try to establish territories near their birthplace, but can geographically expand their search for a suitable vacant territory (Mikkola 1983). Tawny Owls typically breed in tree cavities, often made by the Black Woodpecker *Dryocopus martius*. Sometimes they breed in twig nests of Crow *Corvus corone*, Magpie *Pica pica*, Sparrowhawk *Accipiter nisus* and Buzzard *Buteo buteo*. They readily accept nest boxes and may breed near human settlings (Mikkola 1983, Svensson et. al 1999, König & Weick 2008, own observations). This makes them well suited for scientific studies and this is probably the main reason why the Tawny Owl is one of the most studied species of birds of prey in Europe.

In this paper, we present results on changes in the breeding population size and breeding results between the years 1996 and 2010 as a contribution to the knowledge of the geographical variation of the breeding biology of Tawny Owls.

Methods

The investigation began in the mid-1980s, when the first breeding attempts were recorded in 1987 (Ericsson et al. 2006). It was a modest project the first couple of years, with a long learning curve. The number of nest boxes was high from the start, but many of the boxes were located incorrectly, with high rejection rate as a result. With increased knowledge, nest boxes were relocated to areas more suitable to the preferences of Tawny Owls. Suitable locations have been identified since 1991, and relocations of nest boxes to maximize occupancy have been carried out, more or less, on a yearly basis since then. However, there are 48 territories where the nest boxes have had the same location throughout the study and these territories serve as controls when we estimate the effect of the relocations. The monitoring of breeding females started in 1994. The methods of collecting data have remained unchanged throughout the study.

The study was carried out west of Lake Vättern in the municipalities of Hjo, Karlsborg, Laxå, Tibro, Töreboda and Skövde. The owls in this study bred in a variety of habitats, like deciduous and mixed coniferous forests, but also in larger parks and semi-open pastures. The total geographical area is about 1000 km^2. Within this area, large parts are not suitable as breeding habitats for Tawny Owls.

All nest boxes and natural nesting sites were inspected every year of the study period 1996–2010. A first inspection was made in April–May. When an owl was found breeding, that nest was visited at least three times (to control or ring the females, to ring the young and to clean the nest), but usually more visits than three were needed to collect reliable data on clutch size, hatching results, determine the age of the young. The majority of the monitored owls were breeding in nest boxes, but occasionally breeding owls were found in natural cavities. The nest boxes were placed in trees at a height of 3 to 5 meters, and approximately 1 to 3 km apart. Inside the nest box a layer of sawdust was placed, facilitating better incubation conditions of the eggs.

Females were caught during breeding. Unringed females were ringed (rings Museum of Natural History, Stockholm) and aged up to their third calendar year (CY). Age of unringed adult Tawny Owls could be determined by examining the moult pattern and condition of their secondary wing feathers (Petty 1992, Baker 1993, Peter Sunde, pers comm.). Females older than 3 CY were classified as 4 cy+. Age and condition (based on weight) of captured females were measured.

Eggs and all hoarded prey were monitored during the early stages of the incubation period (usually during the first inspection of the nest). Nestlings were ringed, generally between 18 and 25 days old. At ringing, we also measured the weight and determined the age of the nestlings. The age was estimated by measuring their 4th primary using a scale adapted for young Tawny Owls (Peter Sunde, pers comm.). When the nestlings had left the nest (at 30 to 35 days of age), the nest box was cleared of old nesting material. The nest box was also searched for rings or dead chicks and new sawdust was placed for the next year's breeding.

A breeding attempt was defined as an attempt when at least one egg was found in the nest. A successful breeding attempt was defined as a case when at least one young was ringed. Nesting success was measured as the proportion of successful breeding attempts out of all breeding attempts. Hatching success was measured as the number of hatched young per egg laid.

Each prey found in a nests was identified to species in the field, except for the genera of *Apodemus* (wood mouse or yellow-necked wood mouse *A.*

flavicollis) and *Sorex* (common shrew *S. araneus* or pygmy shrew *S. minutus*), which were identified to their respective genus.

Regression analyses were conducted with STATISTICA 6.0.

Results

The total number of ringed owls between 1987 and 2010 was 3252, including ringed young and breeding adults. Of these birds, 535 were recovered dead or controlled alive. Of the latter, 303 were controlled as breeding females by ourselves. Other people found 220 of our ringed owls dead, and 20 were controlled alive. These latter had been trapped in barns or summerhouses and were released after rehabilitation. During the period of 1996–2010, 925 breeding females were ringed and monitored. Age is known for 572 of them (Table 1). This number also includes breeding females that have been monitored in subsequent years. Uncontrolled and controlled females, with known and unknown age, varied during the period. Only in 1996 did the number of uncontrolled females exceed the number of controlled females. After 2001, the proportion of controlled females stabilised, and no less than 80 % was controlled each year (Table 1). The proportion of females with known age was low during the early years but since 2001 it has always been 50% or better (Table 1).

Population

The total breeding population, with all nest boxes included, varied with peaks in 2003, 2008 and 2010 (Figure 1). The mean number of young per successful breeding was 2.34. The mean number of breeding attempts per year was 74, the mean number of eggs laid per year was 259, and the mean number of ringed young per year was 174 (Table 2). The number of breeding attempts as well as the number of successful breeding attempts was highest in 2010 (108) and lowest in 1996 (23) (Table 2).

The population of breeding owls showed a significant positive trend in the area over the whole study period (regression analysis, $R= 0.84$, $R^2= 0.70$, Adjusted $R^2=0.68$, $F(1,13)=30.23$, $p<0.01$) (Figure 2). The main increase occurred during the first part of the period. When considering only the 48 territories without any relocation of nest boxes, we found

Table 1. The number of breeding females during 1996–2010. Uncontrolled females are females that could not be controlled during breeding. Females with known age are those that were ringed as nestlings or as breeding adults through their third calendar year. Females with unknown age are those that were ringed as breeding adults older than in their third calendar year.
Antal häckande honor 1996–2010. Okontrollerade honor är honor som inte kunde kontrolleras under häckningen. Honor med känd ålder är honor som märkts som boungar eller som häckande till och med tredje kalenderåret. Honor med okänd ålder är honor som märkts som häckande senare än under tredje kalenderåret.

Year *År*	Breeding attempts *Häcknings-försök*	Uncontrolled females *Ej kontrollerade honor*	Controlled females *Kontrollerade honor*	Females of known age *Honor med känd ålder*	Famales of unknown age *Honor av okänd ålder*
1996	23	16	7	3	4
1997	33	13	20	1	19
1998	48	11	37	10	27
1999	64	27	37	20	17
2000	52	13	39	18	21
2001	76	6	70	40	30
2002	87	11	76	48	28
2003	104	20	84	52	32
2004	63	12	51	35	16
2005	92	12	80	51	29
2006	94	8	86	59	27
2007	87	10	77	58	19
2008	106	18	89	69	20
2009	79	6	68	50	18
2010	108	4	104	58	46
Total	1117	187	925	572	352

Breeding habitat for Tawny Owls.
Kattugglebiotop. Foto: Lars-Ove Nilsson.

Breeding habitat for tawny owls.
Kattugglebiotop. Foto: Lars-Ove Nilsson.

Nesting box for Tawny Owls.
Holk för kattuggla. Foto: Peter Ericsson.

Female Tawny Owl, 3 cy+.
Hona av kattuggla, 3k+. Foto: Peter Ericsson.

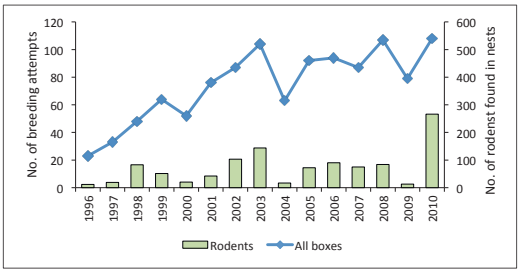

Figure 1. Number of breeding attempts (blue dots) and prey abundance (total number of prey items found in active nests; green bars) between 1996 and 2010.
Antal häckningsförsök (blå prickar) och bytesantalen (totala antalet byten påträffade i aktiva bon; gröna staplar) mellan 1996 och 2010.

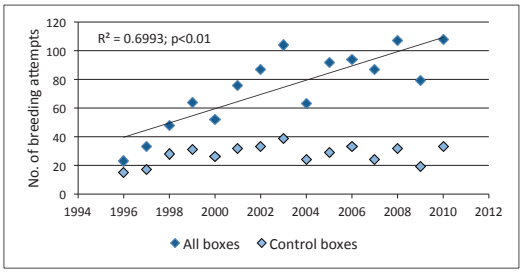

Figure 2. Upper, dark blue squares: Number of breeding attempts in all territories, including those where nest boxes have been relocated from poor sites to areas with habitat more suitable for tawny owls, as well as in 48 territories where the nest boxes were never relocated (control boxes). Lower, light blue squares: Number of breeding attempts in the 48 control territories where no relocation of nest boxes has been made.
Mörkblå kvadrater upptill: Antal häckningsförsök i samtliga revir, såväl i de där holkar flyttats från sämre till bättre kattugglebiotoper som i de 48 revir där ingen holkflyttning skett. Ljusblå kvadrater nertill: Antal häckningsförsök i de 48 kontrollholkar som aldrig flyttats om inom sina revir.

Table 2. Breeding results during 1996–2010. N=number of controlled nest boxes and natural cavities. Territories are the number of potential territories that could have had breeding Tawny Owls. Nesting success is the proportion of successful breeding attempts. Hatching success is the number of hatched young per laid egg.
Häckningsresultat 1996–2010. N=antal kontrollerade holkar och naturliga håligheter. Revir är antalet potentiella revir som kunde ha haft häckande kattugglor. Häckningsframgång är andelen kullar med minst en ringmärkt unge av samtliga häckningsförsök. Kläckframgång är andelen kläckta av alla lagda ägg.

Year *År*	N	Territories *Revir*	Breeding attempts *Häcknings-försök*	Occup-ancy *Andel bebodda*	Successful *Lyckade*	Nesting Success *Häcknings-framgång*	Eggs *Ägg*	Ringed young *Märkta ungar*	Hatching success *Kläck-framgång*
1996	176	170	23	14%	15	65%	67	40	60%
1997	172	168	33	20%	18	55%	99	51	52%
1998	171	170	48	28%	36	75%	189	126	67%
1999	171	168	64	38%	58	91%	246	194	79%
2000	174	172	52	30%	34	65%	139	80	58%
2001	174	171	76	44%	57	75%	269	172	64%
2002	179	175	87	50%	74	85%	324	235	73%
2003	181	177	104	59%	82	79%	365	255	70%
2004	184	178	63	35%	43	68%	155	97	63%
2005	183	179	92	51%	80	87%	329	252	77%
2006	187	182	94	52%	72	77%	379	242	64%
2007	188	184	87	47%	70	80%	311	194	62%
2008	192	185	107	58%	83	78%	364	242	66%
2009	195	187	79	42%	63	80%	209	140	67%
2010	201	196	108	55%	86	80%	439	291	66%
Mean	182	177	74	42%	58	76%	259	174	66%
Total	2728	2662	1117		871		3884	2611	

no significant increasing trend in population size (regression analysis, R= 0.32, R^2= 0.10, Adjusted R^2=0.03, F(1,13)=1.49, p=0.24) (Figure 2).

Breeding results

The number of ringed young has varied considerably over the years, with peaks in 2003, 2005 and 2010. The highest number of ringed nestlings (291) was recorded in 2010 and the lowest number (40) in 1996. In two seasons (2000 and 2004), the number of ringed chicks was less than 100 (Table 2). Hatching success was highest in 2005 when 77 percent of the eggs hatched. However, the proportion of successful breeding attempt was highest in 1999, when 91 percent of the breeding attempts were successful (Table 2). There was a significant positive correlation between nesting success and population density (regression analysis, R= 0.66, R^2= 0.44, Adjusted R^2=0.40, F(1,13)=10.27, p<0.01) (Figure 3).

Prey

Nine different species of mammalian prey were found in the nest boxes during the study period (Table 3). The two most common prey species were bank vole and field vole followed by pooled number for the two species of wood mouse. Peak years for bank vole occurred in 1998, 2002 and 2010. Peak years for field vole were recorded in 2003, 2006 and 2010. Peaks of wood mice were recorded in 2008 and 2010. All these three taxa had a peak in 2010. A total of 266 different rodent specimens were recorded in 2010, which is the highest number ever during the study.

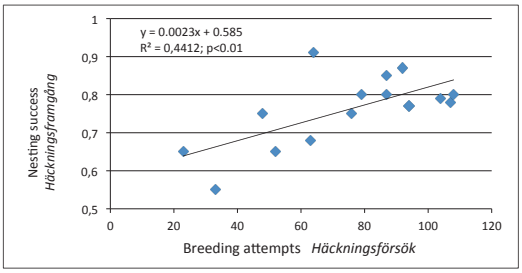

Figure 3. Relationship between nesting success and number of breeding attempts.
Förhållandet mellan häckningsframgången och antalet häckningsförsök.

Discussion

The population increase during the first part of the study period may have had two reasons. First, the population size may have been low before the start of the study and the increase a delayed effect from the presence of a large number of nest boxes already when the study started in 1996. Second, the relocation of nest boxes to more suitable habitats within the territories may have attracted the pairs to use nest boxes instead of natural cavities. Although the majority of nest box relocations were made before 2001, relocations have also been made in later

Table 3. Number of mammalian prey recorded in nest boxes between 1996 and 2010.
Antal däggdjursbyten i holkarna mellan 1996 och 2010.

Year	*Clethrionomys glareolus*	*Microtus agrestis*	*Apodemus sp.*	*Sorex sp.*	*Arvicola terrestris*	*Muscardinus avellanarius*	*Mus musculus*	*Talpa europaea*	*Rattus norvegicus*	Total
1996	10	0	0	0	0	1	1	0	0	12
1997	9	1	0	1	5	1	0	1	1	19
1998	65	0	1	2	9	5	0	0	1	83
1999	26	6	1	10	4	1	2	1	0	51
2000	7	0	0	2	5	2	2	2	0	20
2001	11	0	19	6	6	0	0	0	0	42
2002	60	4	13	8	8	7	1	2	0	103
2003	40	63	18	5	16	0	0	1	1	144
2004	1	2	6	4	4	0	0	0	0	17
2005	18	13	17	6	13	3	1	0	1	72
2006	21	47	4	4	10	2	0	2	0	90
2007	16	8	15	13	14	7	0	0	2	75
2008	23	12	26	13	7	3	0	0	0	84
2009	1	3	2	1	5	0	0	0	1	13
2010	59	129	25	39	4	6	0	2	2	266
Total	367	288	147	114	110	38	7	11	9	1091
Mean	24,5	19,2	9,8	7,6	7,3	2,5	0,5	0,7	0,6	72,7

years but not to the same extent. After about 2001 the breeding population has not responded to the relocations in a similar way as in the early part of the period, and the population increase has leveled off and seems now to be governed mainly by the abundance of rodents. As we found a significant population increase when we included all nest boxes but not when we included only the forty-eight nest boxes that had never been relocated and hence already from the start were located in good habitat, we conclude that the main factor for the population increase was the relocation of the nest boxes. Possibly, there might also have been a combination of low owl numbers and relocation of nest boxes during the early part of the study period. Perhaps the area became saturated with breeding owls so that relocation of nest boxes no longer could have any effect even if they were place in successively better habitats.

Despite the harsh weather conditions during the winter 2009–2010, the Tawny Owls began to breed in large numbers in 2010. A total of 129 field voles, twice as many as in any previous year was found in the nests of breeding owls. This high number of prey appears to be a consequence of the deep snow cover during the winter of 2009–2010. As suggested by Hörnfeldt (2004), we believe that the field voles were able to forage and reproduce under safe conditions from attacking predators from above. The numbers of breeding attempts, eggs laid and ringed young reached record levels in 2010. The most important factor of this high breeding numbers seems to be the high abundance of the most important vole species, bank and field vole and wood mice. For the first time, these species shared a common peak year in 2010.

It is interesting that not only the density of owls but also their nesting success increased when the nest boxes were relocated to better habitats. This is surprising as increasing density is normally assumed to cause food scarcity and increasing competition and then declining breeding success. The explanation of the unexpected effect is probably that the effect of food abundance variation is sufficiently strong to conceal the effect of competition so that in good rodent years both the number of breeding owls and their breeding success increase.

The mean brood size reported in this study showed no big differences from that in other studies in Europe (e.g. Southern 1970, Mikkola 1983, Petty 1987, Persson 2003). We found a mean value of 2.3 young/brood (successful breeding attempt), which can be compared with 1.96 young per brood in England (n=76, Southern 1970) and 2.1 young per brood in Sweden (n=18, Persson 2003). Mikkola (1983) gives the following average brood sizes: 3.05 (n=601) in Finland, 2.61 (n=131) in Central Europe and 2.27 (n=181) in Britain. Southern (1970) states that the optimum brood size of Tawny Owls is two young per brood. His main argument is that growth rate (weight increase per chick and day) decreases with number of chicks in the brood. Our results support his theory, but before it can be fully accepted, other factors must be controlled, such as age and breeding experience of the breeding pair.

Acknowledgements

The study of Tawny Owls was supported by Elis Wides foundation, Swedish Ornithological Society. We express our thanks to Sören Svensson, Robert Ekblom, Ulf Wiktander and two anonymous referees for valuable criticism on an early manuscript. We also thank Karin Gällman, Lisa Malm and Kurt Henriksson for the great assistance during fieldworks. Special thanks to all the landowners, who allowed us access to set up nest boxes and the ongoing monitoring work on their property.

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Sammanfattning

I många fågelpopulationer har man hittat ett samband mellan häckningsframgång och födotillgång. I synnerhet gäller detta för predatorer som rovfåglar och ugglor. Kattugglor livnär sig på olika typer av djur, men främst på smågnagare, och antalet häckande par varierar mellan åren beroende på hur mycket bytesdjur det finns inom reviren. Under gnagartoppar kan kattugglorna få stora kullar. När gnagartillgången avtar kan kattugglor byta till alternativa byten, till exempel fåglar och groddjur men även skalbaggar och daggmaskar kan ingå i menyn.

I denna studie häckade kattugglorna i holkar. Studien genomfördes väster om Vättern, i kommunerna Hjo, Karlsborg, Laxå, Tibro, Töreboda och Skövde. Till en början var projektet blygsamt med ganska få häckningar de allra första åren. Antalet holkar var högt från början, men många var felplacerade och antalet häckningar var också lågt till en början. Allteftersom kunskapen om kattugglorna ökade flyttades holkar till områden som är mer lämpade för arten. Lämpliga miljöer för kattuggla har identifierats sedan 1991, och omplaceringar av holkar har utförts, mer eller mindre, varje år sedan dess. Det finns 48 områden som är oförändrade, alltså revir där inga omplaceringar har utförts.

Ägg och de bytesdjur som fanns i holken räknades vid det första besöket. Ungar ringmärktes då de var mellan 18 och 25 dagar gamla. När ungarna hoppat ut ur holken och lämnat boet rensades den från gammalt bomaterial och ett lager kutterspån lades i holken. Alla bytesdjur identifierades i fält, förutom släktena inom *Apodemus* (större skogsmus och mindre skogsmus) och *Sorex* (vanlig näbbmus och dvärgnäbbmus), som identifierades till respektive släkte.

Det totala antalet ringmärkta ugglor mellan 1987 och 2010 var 3252. Av dessa har 535 återfunnits döda eller kontrollerats levande. Under perioden

har 925 honor ringmärkts och studerats. Åldern är känd hos 572 av dem.

Antalet påbörjade häckningar varierade under perioden, med toppar under 2003, 2008 och 2010. Det genomsnittliga antalet ungar per häckning var 2,34. Antalet påbörjade häckningar var 74 i genomsnitt, antalet ägg 259 och ringmärkta ungar per år var 174. Antalet häckningsförsök liksom antalet lyckade häckningsförsök var högst i 2010 (108) och lägst 1996 (23).

Antalet ringmärkta ungar har varierat mellan åren, där de högsta topparna registrerades under 2003, 2005 och 2010. Sistnämnda år ringmärktes det högsta antalet ungar (291) under perioden medan 1996 hade det lägsta antalet märkta ungar (40). Häckningsframgången var störst 2005 då 77 procent av äggen kläcktes. Andelen lyckade häckningsförsök var störst 1999, då 91 procent av de häckande paren lyckades.

De två vanligaste bytesdjuren som observerades i holkarna var åkersork och skogssork. Toppåren för skogssork inträffade 1998, 2002 och 2010. Toppåren för åkersork registrerades under 2003, 2006 och 2010. Toppar av skogsmöss inföll under 2008 och 2010. Alla dessa tre taxa hade en topp under 2010.

Trots de svåra väderförhållanden under vintern 2009–2010, började kattugglor häcka i stort antal under 2010 då tillgången på sork var mycket god. Den viktigaste faktorn i den höga siffran under 2010 verkar bero på den goda förekomsten av de viktigaste bytesarterna, åker- och skogssork samt skogsmus.

Kattugglepopulationen visade en positiv signifikant trend i området under studieperioden. Om man endast ser till de 48 revir där inga omlokaliseringar av holkar skett, kunde inte samma signifikanta trend ses.

Det är intressant att inte bara tätheten av häckande ugglor, utan också häckningsframgången ökade när holkar flyttades till mer lämpliga miljöer för kattuggla. Detta är särskilt förvånande eftersom en ökande densitet av häckande fåglar normalt antas orsaka födobrist, ökad konkurrens samt sjunkande häckningsframgång. Förklaringen till denna oväntade effekt beror sannolikt på att effekten på god födotillgång är tillräckligt stark för att dölja effekterna av konkurrensen, då antalet häckande ugglor samt häckningsframgången ökade då tillgången på föda var god.

Den genomsnittliga kullstorlek som rapporteras i denna studie visade inga stora skillnader från det som andra studier i Europa tidigare rapporterat. Vi hittade ett medelvärde på 2,3 ungar/kull, vilket kan jämföras med 1,96 ungar/kull i England (n = 76) och 2,1 ungar per kull i Sverige (n = 18). Mikkola (1983) ger följande genomsnittliga avkommor storlekar: 3,05 (n = 601) i Finland, 2,61 (n = 131) i Centraleuropa och 2,27 (n = 181) i Storbritannien. Southern (1970) påstår att den optimala kullstorleken hos kattugglor är två ungar per kull. Hans huvudargument är att tillväxttakten (viktökning per unge och dag) minskar med antalet ungar i kullen. Våra resultat stödjer denna teori men innan den kan accepteras fullt ut, måste andra faktorer kontrolleras, som exempelvis ålder och tidigare häckningserfarenhet av det häckande paret.