

Incubation period behaviour of a pair of Eurasian Eagle-owls (*Bubo bubo*) based on IR-video recordings at a nest site in Baden-Württemberg, Germany in 2015

Comportamento de um casal de bufo-real (*Bubo bubo*) durante o período de incubação com base em gravações de vídeo de infravermelhos num ninho em Baden-Württemberg, Alemanha, em 2015

Christian T. Harms^{1*}

¹ Deutsche Arbeitsgemeinschaft zum Schutz der Eulen (AG Eulen; www.ageulen.de), Brandensteinstr. 6, D-79110 Freiburg, Germany

* Corresponding author: cth-frbg@go4more.de



ABSTRACT

Incubation period behaviours displayed by a pair of Eurasian Eagle-owls (*Bubo bubo*) at a nest site in Southern Germany were captured by infrared (IR) video camera in 2015. During 41 days of incubation, the female left the nest site 169 times for self-maintenance (defecation, feeding, preening, stretching, regurgitation of pellets). Her absences averaged 21 min per night, totalled 14:27 h and were analyzed in detail. The timing and behavioural context of 677 egg turning incidents were evaluated. During incubation the transfer of prey was conspicuous, and their timing and the owl's behaviours were described. Most of the 111 prey items delivered by the male were rodents (66%) including voles (*Arvicolinae* including *Microtus* spp.) and also some birds (10%). Prey delivery was variable and the female experienced temporary food shortages. Thirty-one copulation attempts by the male during the incubation period were rejected by the female and coincided with reduced prey deliveries to the female. This report is the first detailed and comprehensive account of the behaviours displayed by a pair of Eurasian Eagle-owls at their nest during incubation under natural conditions.

Keywords: *Bubo bubo*, Eagle-owl, incubation, IR-video recording, nest site behaviour

RESUMO

O comportamento exibido por um casal de bufo-real (*Bubo bubo*) durante o período de incubação num ninho no sul da Alemanha foi gravado através de uma câmara de vídeo de infravermelhos em 2015. Durante os 41 dias de incubação, a fêmea deixou o ninho 169 vezes para auto-manutenção (defecação, alimentação, *preening*, exercício e regurgitação). As suas ausências demoraram em média 21 minutos por noite, totalizando 14h27, e foram analisadas em detalhe. O período de ocorrência e contexto de 677 comportamentos de mobilização dos ovos foram avaliados. Durante a incubação, a transferência de presas foi conspícua, e o seu período de ocorrência e comportamento associado foram descritos. A maioria dos 111 itens de presas entregues pelo macho eram roedores (66%), incluindo ratos-cegos (*Arvicolinae* incluindo *Microtus* spp.), e também algumas aves (10%). A entrega de presas foi variável e a fêmea passou por períodos de privação de alimento. Trinta e uma tentativas de cópula pelo macho durante o período de incubação foram rejeitadas pela fêmea e coincidiram com a redução de entrega de presas à fêmea. Este estudo é o primeiro relato detalhado e abrangente dos comportamentos exibidos por um casal de bufo-real em condições naturais, durante a incubação.

Palavras-chave: *Bubo bubo*, bufo-real, comportamento no ninho, incubação, vídeo de infravermelhos

Introduction

The use of photo and video recording techniques to study birds has recently increased with the advancement of associated micro-electronic technology (Ribic et al. 2012). Nest-site predation (Bolton et al. 2007; Renfrew & Ribic 2003) and food delivery to raptor chicks (see references listed in Harms 2018a) are the most prominent topics studied using this technology. Quite surprisingly, there are few studies on owls even though affordable infra-red (IR) cameras have been available for several years. IR video recording is best used to study behaviour at fixed locations such as nest sites. Harms (2021a) listed numerous webcams that have used IR-cameras to monitor the nests of various owl species (i.e., www.uhu.webcam.pictura.de/tagebuch), including Eurasian Eagle-owls (*Bubo bubo*; hereafter Eagle-owl), for public viewing but there are no published studies from these projects.

Nielsen et al. (2015) employed video camera technology to study Eagle-owl prey delivery to chicks at a nest site in Denmark. In 2014, I started an IR video recording project to record and analyse behaviour of breeding Eagle-owls from courtship through chick rearing in Baden-Württemberg, Germany (Harms 2017ab, 2018ab, 2019) including pre-incubation behaviours (Harms 2017a, 2021a) and prey delivery and diet (Harms 2018a). Here I present an analysis of Eagle-owl behaviour during the incubation period.

Table 1 - Summary information on the IR-video recordings of incubation period behaviour of a pair of Eurasian Eagle-owls (*Bubo bubo*) at a nest site in Baden-Württemberg, Germany in 2015.

* time between sunset and sunrise, including dusk & dawn periods

Tabela 1 - Resumo das informações sobre as gravações em vídeo de infravermelhos do comportamento de um casal de bufo-real (*Bubo bubo*) durante o período de incubação, num ninho em Baden-Württemberg, Alemanha, em 2015.

PERIOD	INCUBATION
Date	Feb 22 - Apr 3
Calendar days	41
Recording days	41
Hours recorded [h:min]	699:10
night time hours recorded* [h:min] (% of total)	495:57 (70.9)
daytime hours recorded [h:min] (% of total)	203:13 (29.1)
avg. recording time per recording day [h:min]	17:03

Table 2 - Estimated timing of egg laying and hatching based on IR-video recordings of a pair of Eurasian Eagle-owls (*Bubo bubo*) at a nest site in Baden-Württemberg, Germany in 2015.

Note: switching from CET (Central European Time; UTC+1) to CEST (Central European Summer Time; UTC+2) occurred on March 29, 2015 at 2:00 o'clock

* based on time of first and last sighting

Tabela 2 - Datas estimadas da postura e eclosão dos ovos, referentes a um casal de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, com base em imagens de vídeo de infravermelhos, obtidas em 2015.

	EGG #1	EGG #2	EGG #3
First sighting [date / time]	Feb 22 / 18:20	Feb 25 / 2:05	Feb 28 / 18:18
Last sighting [date / time]	Mar 27 / 22:06	Mar 29 / 20:02	Apr 4 / 8:34
Egg laying interval* [h after previous]	--	55:45	88:13
Hatching interval* [h after previous]	--	44:56	132:32
Duration of incubation [d]	33	32	35

Methods

Behaviours of a pair of Eagle-owls were recorded by means of an IR-video camera directed at their nest site located approx. 25 km West of Freiburg, Baden-Württemberg, Germany (Harms 2017a, 2018b, 2021a). The camera was installed prior to the onset of courting activities in November 2014 and was operated from December 2014 to early June 2015 when the fledglings permanently

wandered off the nest. Details of the nest site, the equipment used in this study and the procedures used in the assessment of the videos have been described in Harms (2021a). Some of the technical complications encountered in the selection and operation of surveillance cameras have been discussed in Harms (2015). Prey species were identified from video recordings to genus when possible.

The biomass of prey delivered was estimated according to Plass (2010), Leditznig (2005) and Schweiger & Lipp (2011). Unidentified items were small and eaten by the female at the nest. These were assumed herein to be 25 g mice to calculate estimated prey biomass. Statistical methods followed McDonald (2014).

Results

The nest site location and IR-video recording setup enabled the daily exchange of batteries and storage media without disturbing the owls, particularly the female during incubation (Harms 2017a, 2018b) and rearing of the chicks (Harms 2019). For several years, the resident pair of Eagle-owls (identified from unique plumage markings visible on the recordings) have reared young at this site. They are part of a small local population that are regularly monitored (Harms 2016, 2018b, Harms & Lühl 2017, Harms et al. 2015).

During the incubation period all nighttime and most daytime hours were recorded (Table 1). The onset of incubation brings about a fundamental behavioural change at the nest site. In the pre-incubation (courting) period the nest site remained empty for 96.6% of nighttime and practically 100% of daytime hours (Harms 2021a). By contrast, during incubation, the female spent all daytime and most of the nighttime hours lying in the nest hollow (Fig. 1).

Egg laying started February 22; the first egg was visible when the female left the nest in the evening at 18:20:25. Dates and times of the laying and hatching are summarized in Table 2 together with laying and hatching intervals as revealed by first and last sightings, respectively, in the video recordings. The switch from CET (Central European Time; UTC+1) to CEST (Central European Summer Time; UTC+2) occurred at 2:00 a.m. on March 29 and has been accounted for in the calculation of the hatching intervals. The

incubation period ended when the last of three eggs hatched in the early morning hours of April 4 (Table 2).

Female Behaviour

During recorded daytime hours the incubating female never left the nest site. From observations made at other Eagle-owl nest sites, incubating females departed only if threatened (Harms 2018c). Attacks by smaller avian predators such as Common Ravens (*Corvus corax*), Carrion Crows (*Corvus corone*) or Eurasian Buzzards (*Buteo buteo*) may be effectively fended off by the female Eagle-owl by assuming a defensive threatening posture such as fluffed plumage and, under heavier pressure, splayed wings (Harms 2015). If predators force a female off the nest, then the eggs or chicks were usually lost to predation (unpubl. data). Using IR-video recordings, I have documented several unsuccessful attacks by predators including Red Fox (*Vulpes vulpes*), European Badger (*Meles meles*) and domestic cat (*Felis catus*) on a female Eagle-owl during incubation (Harms 2018c).

Absences

Despite the female's broodiness, the eggs were not incubated continuously. Each night the female spent time away from the nest in order to take care of bodily needs such as preening or stretching. For the 41-day incubation period, the female was absent 169 times, averaged 4.1 times per night, averaged 5:08 min./absence and the absences totalled 14:27:40 h (Fig. 2). This averaged 21:10 min per night and representing 2.9% of the nighttime hours in the period.

Female absences fell within four distinct categories according to characteristics such as their timing and purpose (Harms 2017b, Table 3) as follows.

(1) **First evening absence.** This behaviour was consistent for 39 days of the incubation period and was female's first nighttime absence. Sixty percent of these departures

Figure 1 - Incubating female Eagle-owl (*Bubo bubo*) in Baden-Württemberg, Germany in 2015.

Figura 1 - Fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação.



Table 3 - Characteristics of a female Eurasian Eagle-owl 's (*Bubo bubo*) absences from a nest site in Baden-Württemberg, Germany in 2015.

Tabela 3 - Caracterização das ausências de uma fêmea de bufo-real (*Bubo bubo*) do ninho, em Baden-Württemberg, Alemanha, em 2015.

CATEGORY	TYPE A	TYPE B	TYPE C	TYPE D
Label	Evening absence	Feeding absence	Intermittent absence	Morning absence
Definition	First absence after sunset	Departing from nest with prey item received from the male	All other absences without a defined recognizable cause	Last absence before sunrise
Purpose	Defecation, pellet removal, self-maintenance	Consumption of large prey items	Self-maintenance	Defecation, pellet removal, self-maintenance
Number within incubation period	39	20	74	36
Number of nights with this activity	39	16	38	36
Total duration [h:min:sec]	3:17:06	3:21:28	5:45:14	2:03:52
Average duration [min:sec]	5:03	10:04	4:37	3:29
Min. / max. duration [min:sec]	1:59 / 20:15	3:00 / 35:00	0:13 / 16:10	1:04 / 10:04
Median duration [min:sec]	3:29	6:33	3:26	3:01

Figure 2 - Number and temporal distribution of absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015.

Figura 2 - Número e distribuição temporal das ausências de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

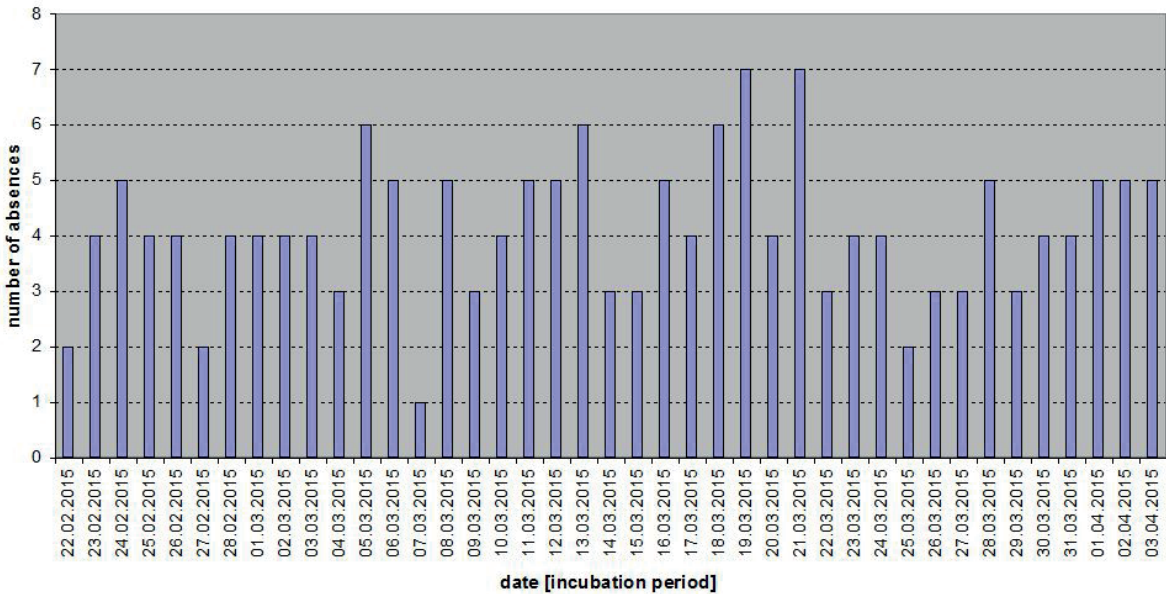


Figure 3 - Duration and temporal distribution of first evening absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015.

Figura 3 - Duração e distribuição temporal das primeiras ausências da noite de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

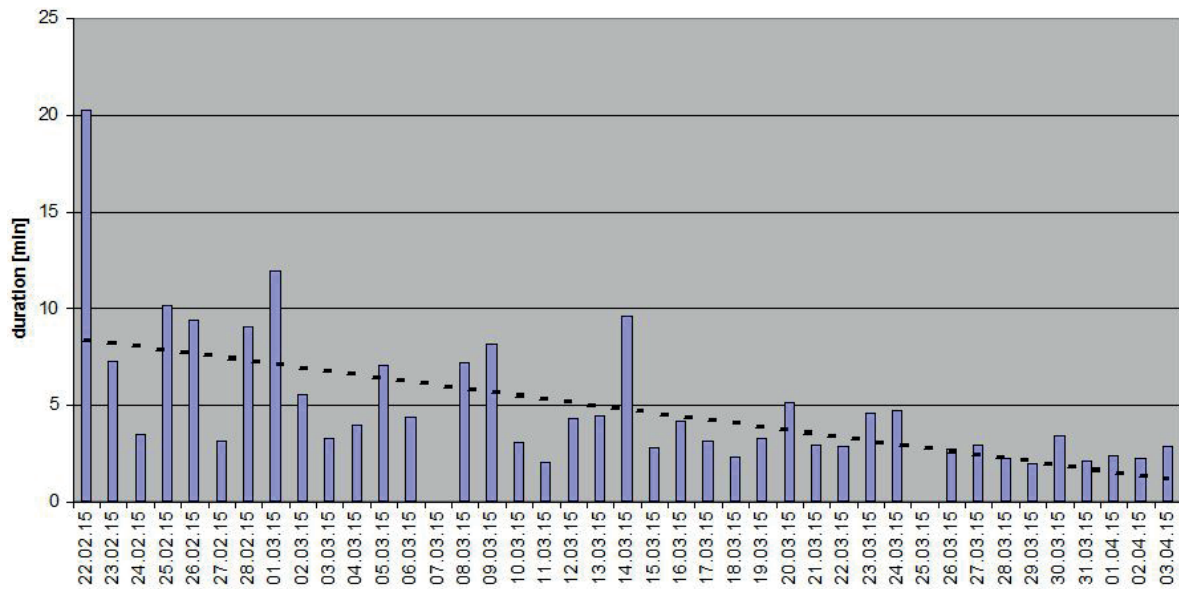


Figure 4 - Duration and temporal distribution of feeding absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015.

Figura 4 - Duração e distribuição temporal de ausências para alimentação de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

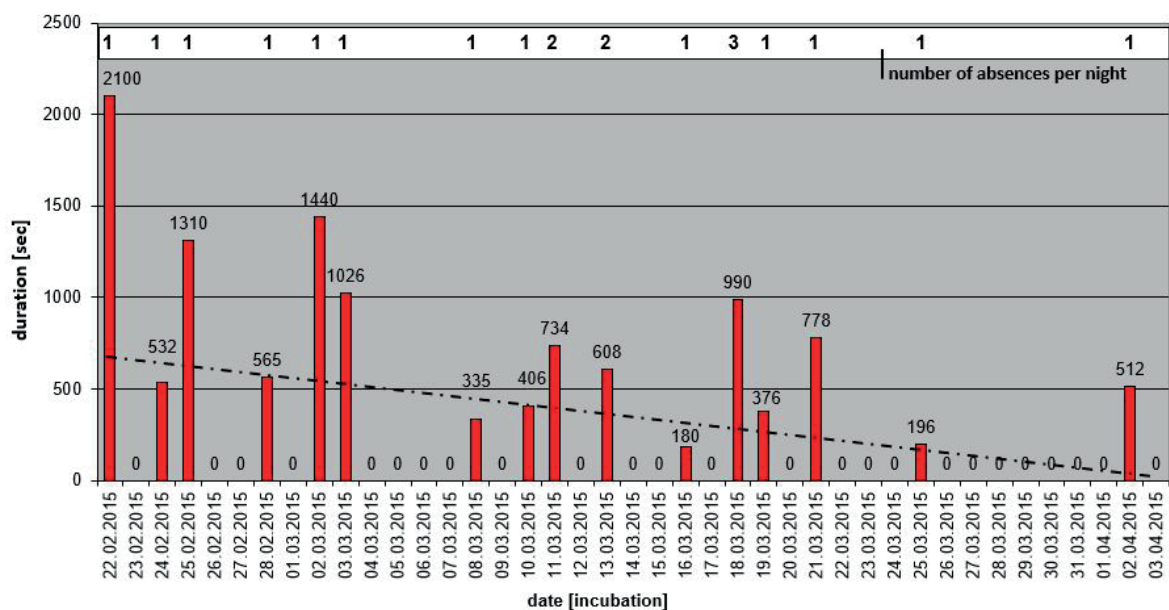
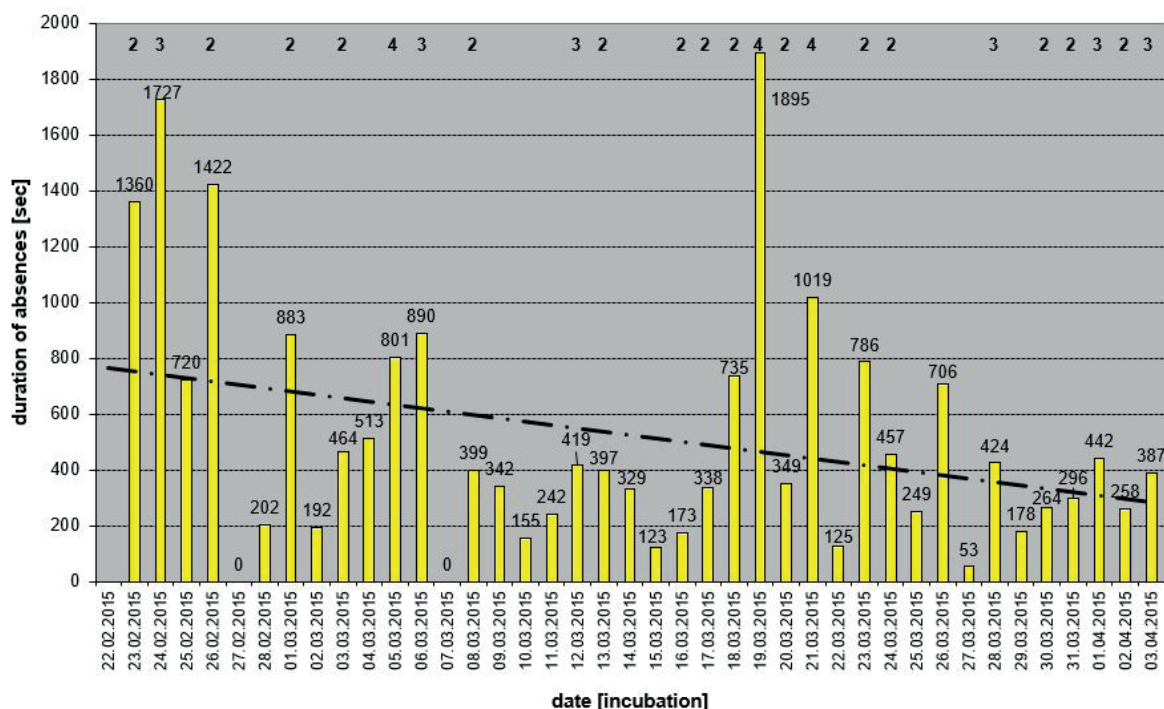


Figure 5 - Duration and temporal distribution of the intermittent absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015. The numbers above columns indicate the number of absences represented by the column.

Figura 5 - Duração e distribuição temporal das ausências intermitentes de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015. Os números acima das colunas indicam o número de ausências representado por essa coluna.



occurred within 30 min after sunset, and 90% within 1 hour after sunset. The earliest was 4:31 min after sunset and the primary purpose of these absences was likely defecation. Unlike many diurnal raptors, the female Eagle-owl was never observed to defecate at the nest site. These absences decreased in duration over the incubation period (Fig. 3).

(2) **Feeding absence.** This absence occurred when the female left to eat larger prey delivered by the male that were too large to swallow whole; such prey were never consumed at the nest site during incubation. The number (20 in 16 nights) and timing and duration of these varied (Figs. 4, 11 & 13) and correlated with the size of the prey item (Fig. 4). Like first evening absences, feeding departures

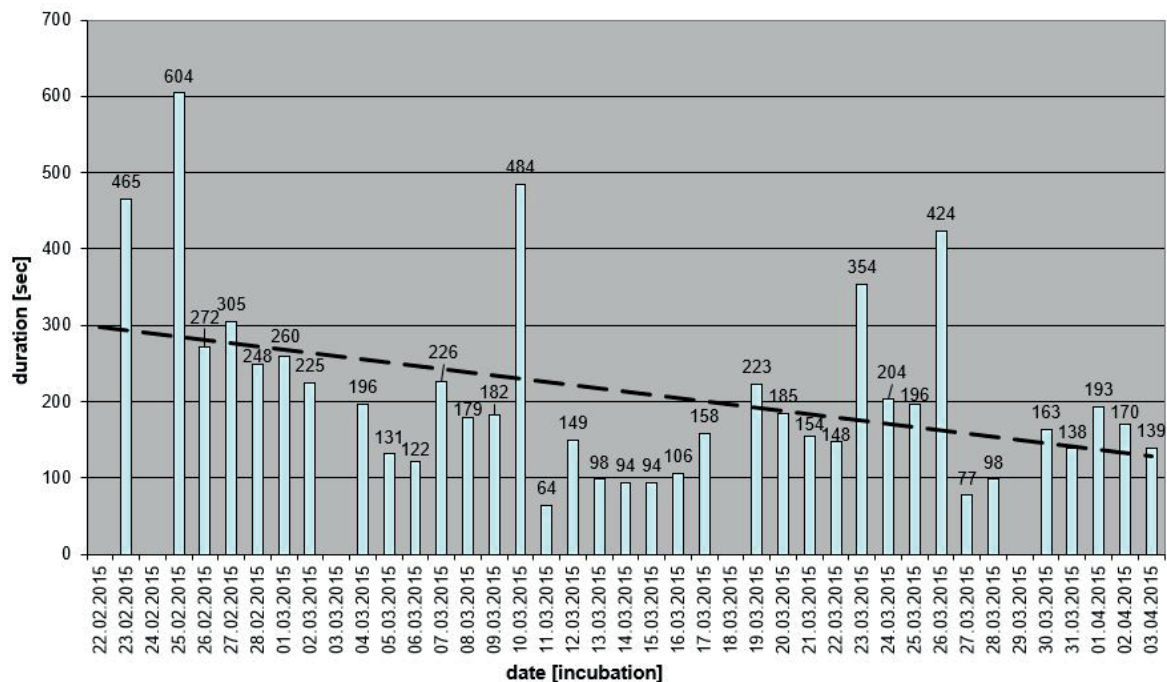
lasted longer during the early stages of incubation and tended to become shorter as the incubation progressed.

(3) **Intermittent absence.** This was the most broadly defined, variable and frequent of the female's absences from the nest site (Table 3). Seventy-four departures totalled 5:45:14 h and averaged 4:37 (\pm 3:29, range 0:13 to 16:10) min. The duration of up to 4 such absences per night decreased over time (Fig. 5) and occurred more often between 3 and 5 o'clock in the morning (unpubl. data).

(4) **Early morning absence.** The last absence of the female before sunrise was likely to defecate; the owls did not defecate at the nest site but did so at specific nearby locations to provide a territorial signal to conspecifics

Figure 6 - Duration and temporal distribution of early morning absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015.

Figura 6 - Duração e distribuição temporal das ausências matinais de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.



(Penteriani & Delgado 2008). The average departure time was 58 (\pm 37) min before sunrise and absences lasted 3.5 min on average. Five early morning absences were associated with eating large prey delivered by the male (not included in Fig. 6 but shown in Figs. 7 and 8) but the female likely also defecated. The duration of these absences also decreased over the incubation period (Fig. 6.).

The number and temporal distribution of all female absence types are presented in Fig. 7 and Fig. 8 represents their duration.

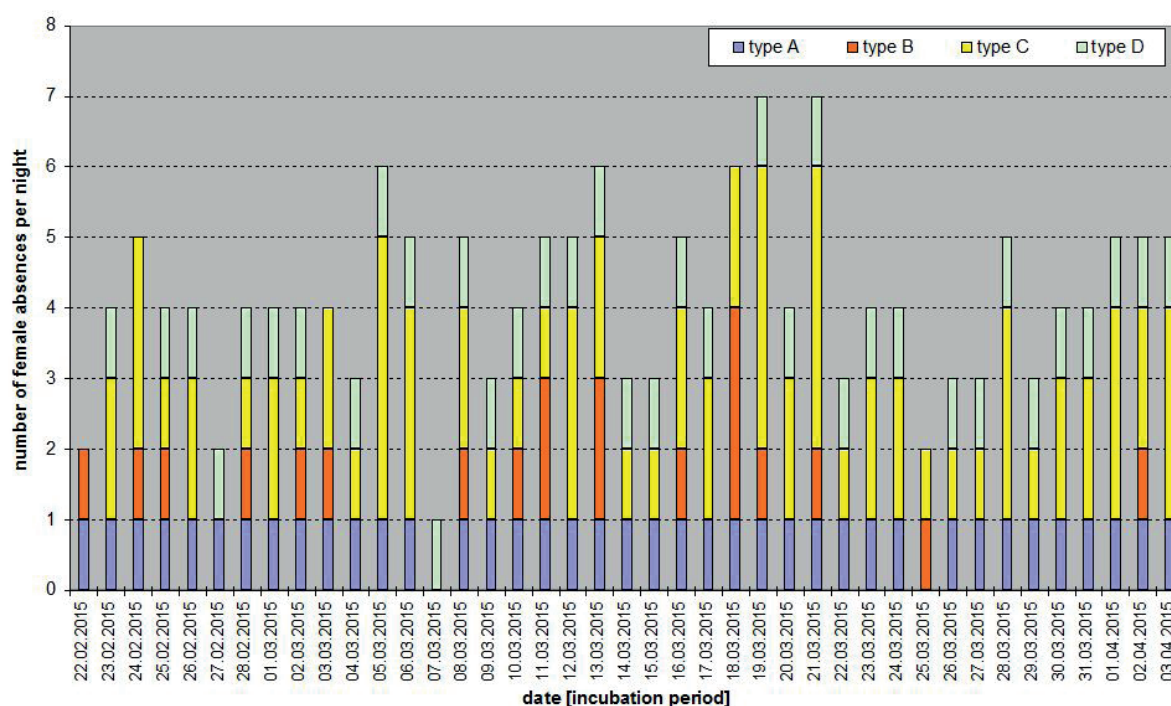
Clutch maintenance, egg turning

The female must protect, shelter and warm the eggs containing the developing embryos. Regular and frequent egg turning ensures they receive warmth from all sides and to keep the egg yolk and embryo suspended, by the chalazae, in the centre of the albumen.

Eggs were turned on average every 57 min during nighttime and less frequently (once every 1:24 h) during daytime (Table 11) and the daily distribution of 677 observed egg turning actions are depicted in Fig. 9. Extrapolated to include the daytime hours which were not recorded, we may expect 880-900 egg turning incidents during the incubation period. Egg turning activities were significantly reduced (Fig. 9) and intervals between turning increased as hatching progressed. Sixty-five percent of the egg turnings were followed by another turning action within 60 min and 84% of all turnings occurred within 90 min of the previous (Fig. 10, n = 636 egg turning events). Eggs were often turned within 2 min following the female's return to the nest after an absence and after a copulation, the consumption of delivered prey, or plumage maintenance (Harms 2017b, Table 5).

Figure 7 - Number and temporal distribution of all absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015. Type A = Evening absence; Type B = Feeding absence; Type C = Intermittent absence; Type D = Morning absence. See Table 3 for more detail on absence type definitions and behavioural context.

Figura 7 - Número e distribuição temporal de todas as ausências de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015. Tipo A = Ausência noturna; Tipo B = Ausência para alimentação; Tipo C = Ausência intermitente; Tipo D = Ausência matinal. Ver Tabela 3 para mais detalhe sobre a definição dos tipos de ausência e contexto comportamental.



Plumage maintenance

Attending to plumage and turning eggs were associated behaviours ('behavioural ensembles') and occurred at least 450 times (Table 5). The number and temporal distribution of feather care by the female was not assessed in detail but there were extended times of low activity as well as times when the female appeared restless or nervous, during which she was engaging in feather care activities much more frequently. On some nights the female was relaxed while on other nights she appeared to be irritated and hyperactive.

Handling of prey

Smaller items (a mouse or vole) were always swallowed on-site and in one piece

and usually shortly after received. Larger items (i.e., moles, rats, larger mammals, birds) were consumed outside the nest (see above). The duration of feeding absences (3 to 35 min) were roughly proportionate to the size of prey delivered (unpubl. data). This changed after eggs hatched when all prey, regardless of their size, were torn apart at the nest and small pieces offered to the chicks. The female consumed small bits while feeding her chicks and swallowed bulky pieces once the chicks were fed. In stark contrast with female behaviour during incubation, surplus feed items were always stored at the nest site for future consumption once eggs had hatched (unpubl. data).

Figure 8 - Cumulative duration of all absences of a female Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015. Type A = Evening absence; Type B = Feeding absence; Type C = Intermittent absence; Type D = Morning absence. See Table 3 for more detail on absence type definitions and behavioural context.

Figura 8 - Duração cumulativa de todas as ausências de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015. Tipo A = Ausência noturna; Tipo B = Ausência para alimentação; Tipo C = Ausência intermitente; Tipo D = Ausência matinal. Ver Tabela 3 para mais detalhe sobre a definição dos tipos de ausência e contexto comportamental.

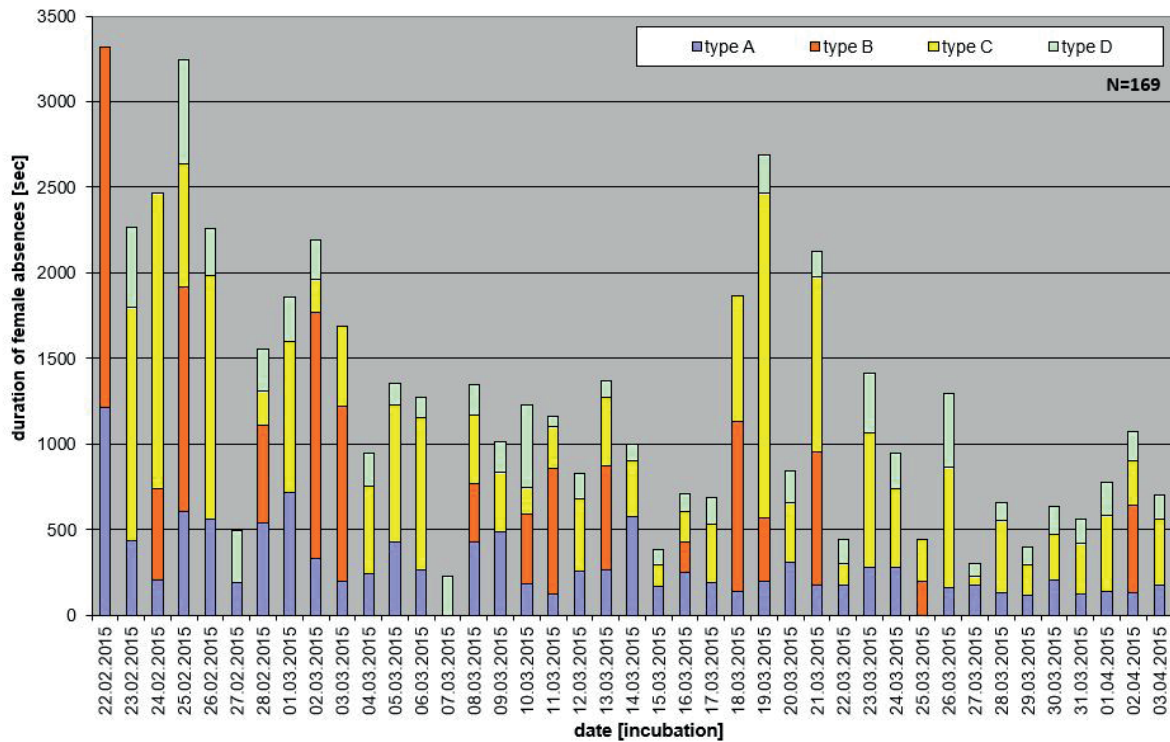


Table 4 - Egg turning behaviour of a female Eurasian Eagle-owl (*Bubo bubo*) at a nest site in Baden-Württemberg, Germany in 2015.

* hours from sunset to sunrise; ** recorded day time hours only

Tabela 4 - Comportamento de viragem dos ovos de uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, em 2015.

RECORDED EGG TURNING (FEB 22 - APR 3)	NIGHT*	DAY**	NIGHT AND DAY
number (%) during incubation period	532 (79)	145 (21)	677
avg. number per day \pm SD	13 \pm 4.4	3.5 \pm 2.9	15.5 \pm 5.6
min. / max. number	3 / 22	0 / 13	3 / 26
median number	14	3	16
avg. time between 2 consecutive egg turnings (N=636) [h:min:sec]	0:56:56	1:24:00	1:01:58

Figure 9 - Number and temporal distribution of egg turning during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 9 - Número e distribuição temporal da viragem de ovos durante o período de incubação num ninho de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, em 2015.

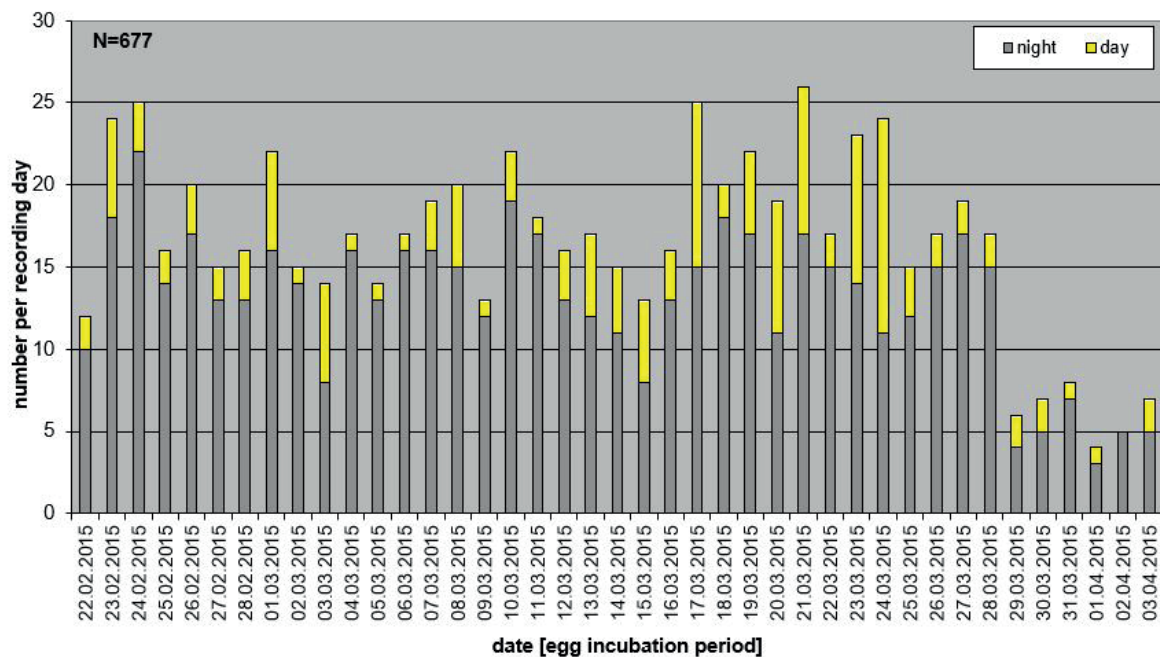


Table 5 - Context of egg turning behaviour of a female Eurasian Eagle-owl (*Bubo bubo*) at a nest site in Baden-Württemberg, Germany in 2015.

Tabela 5 - Contexto do comportamento de viragem dos ovos por uma fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, em 2015

BEHAVIOURAL CONTEXT	RECORDED OCCURRENCE	COMMENTS
Return from absence	160 of 169 absences	Not practiced 4x during incubation & 5x during hatching
Copulations incl. attempted	30 of 37 copulations	
Prey delivered by male and then eaten by female	37 of 80 prey deliveries by male eaten by female	No egg turning in 43 cases (6x during incubation & 37x during hatching)
Preening	450 incidents	

Figure 10 - Time between two egg turning actions within the same night at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 10 - Tempo entre duas ações de viragem de ovos na mesma noite num ninho de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, em 2015.

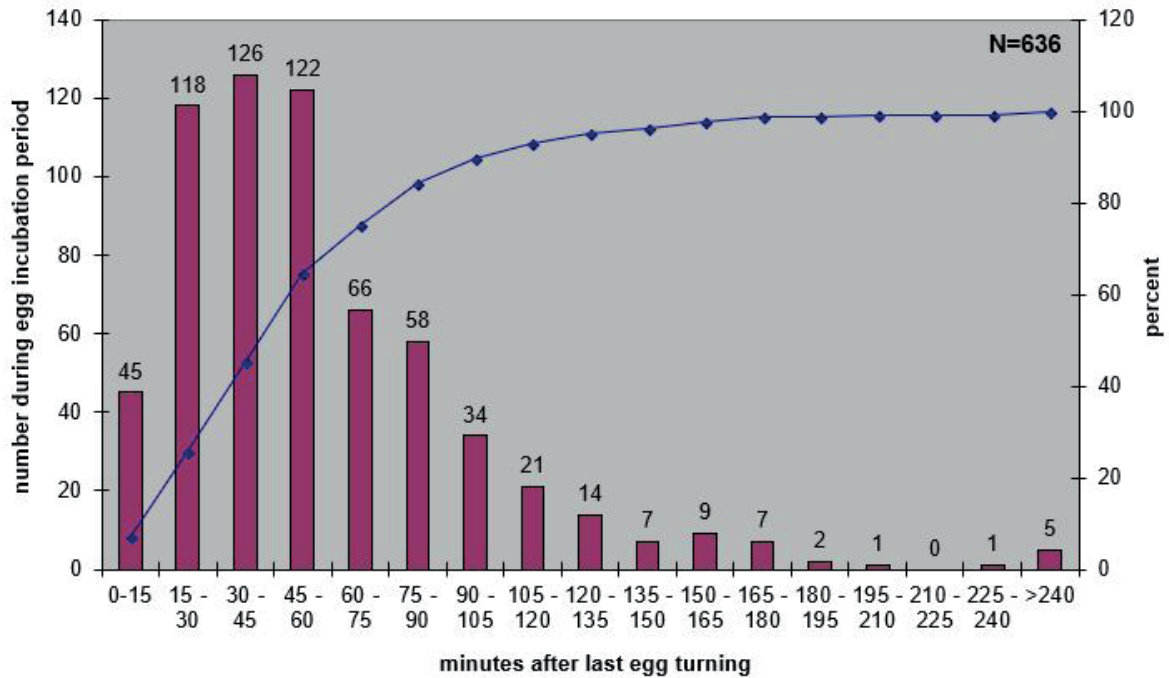


Figure 11 - Number and temporal distribution of prey deliveries by a male Eurasian Eagle-owl (*Bubo bubo*) during the incubation period at a nest site in Baden-Württemberg, Germany in 2015.

Figura 11 - Número e distribuição temporal de entregas de presas pelo macho de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

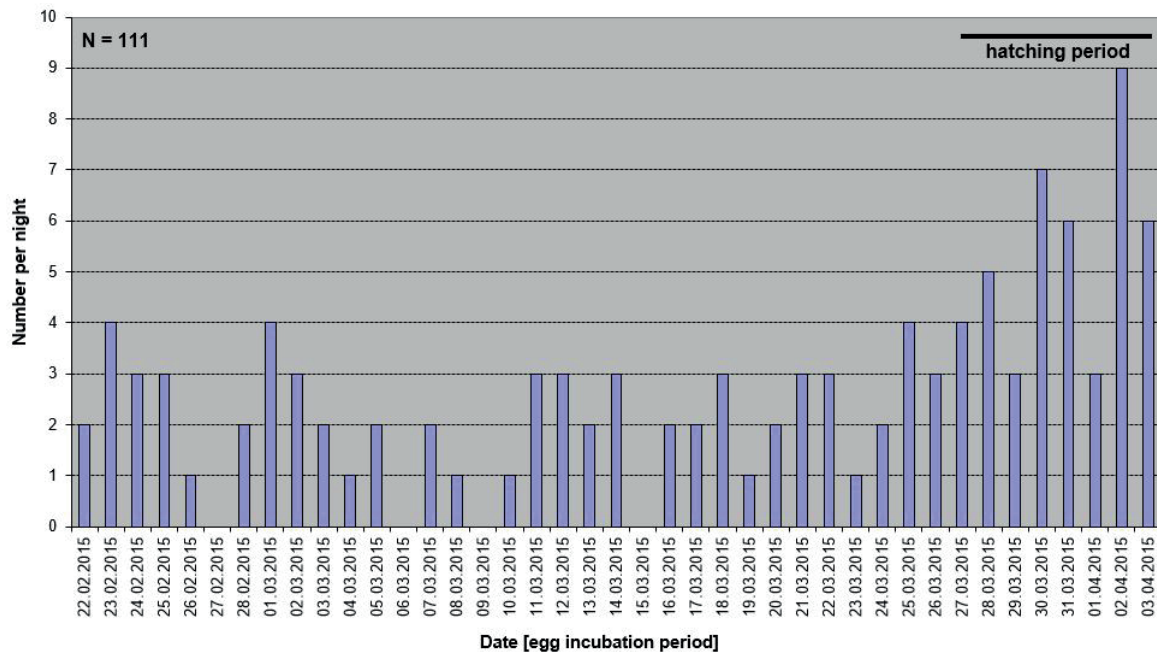


Figure 12 - Timing of the first nocturnal prey delivery during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 12 - Período de ocorrência da primeira entrega de presas da noite durante o período de incubação num ninho de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, em 2015.

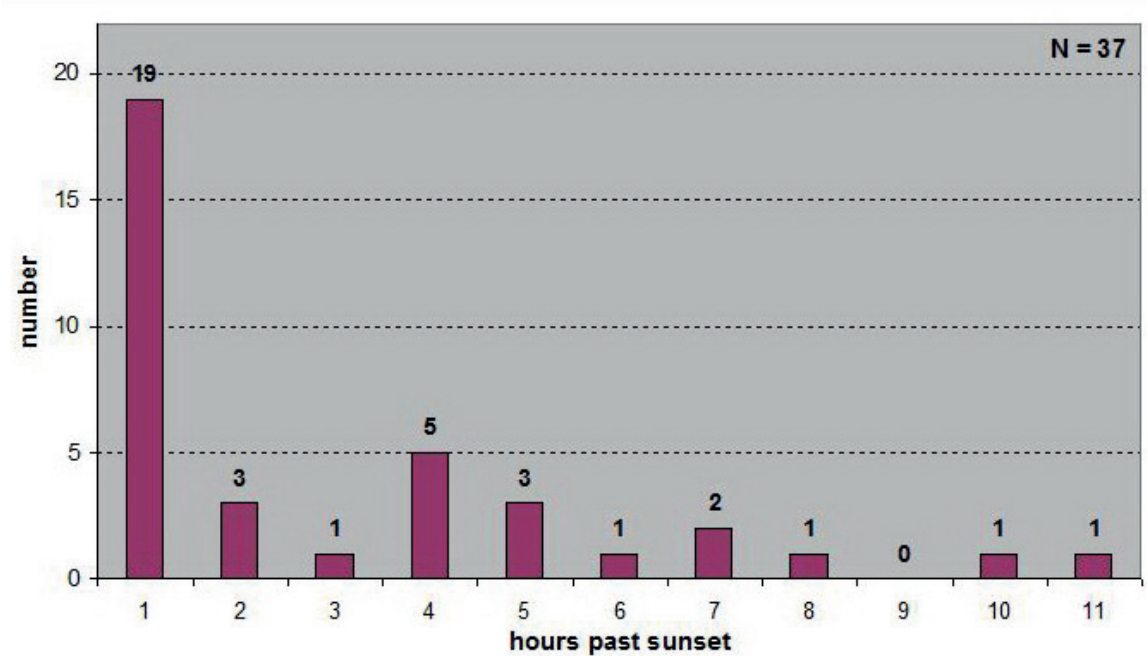


Figure 13 - Time of first prey delivery by date during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 13 - Período de ocorrência da primeira entrega de presas por data durante o período de incubação num ninho de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, em 2015.

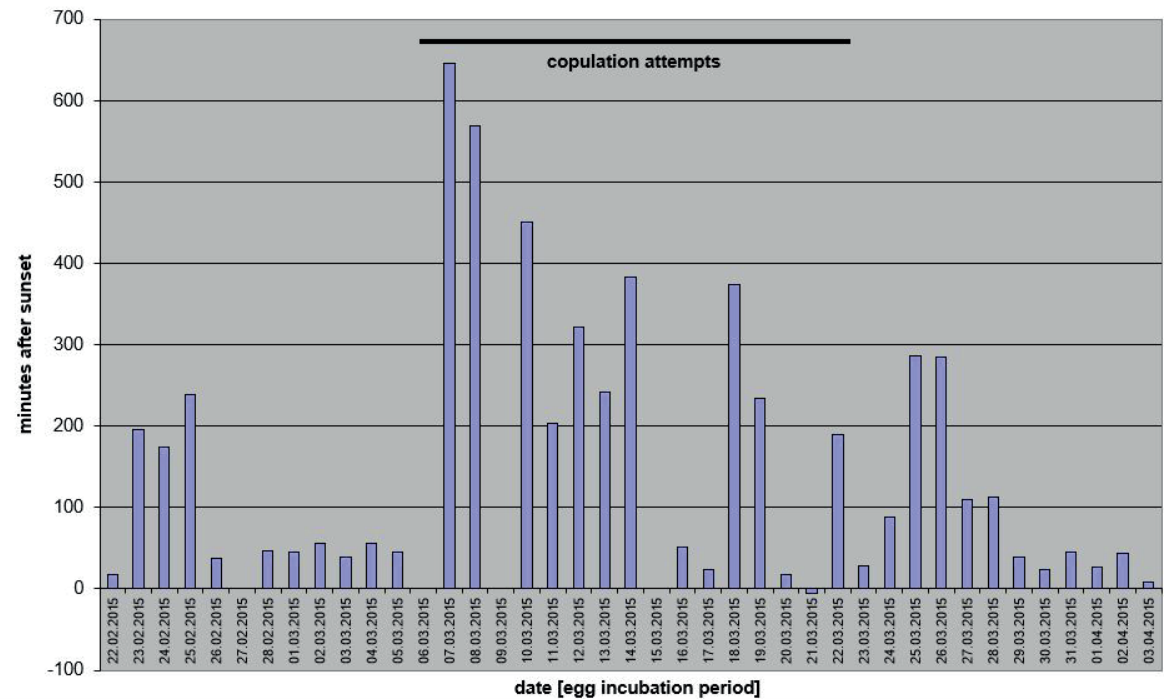


Figure 14 - Time elapsing between two consecutive prey deliveries within the same night during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 14 - Período de tempo entre duas entregas de presas consecutivas na mesma noite durante o período de incubação num ninho de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, em 2015.

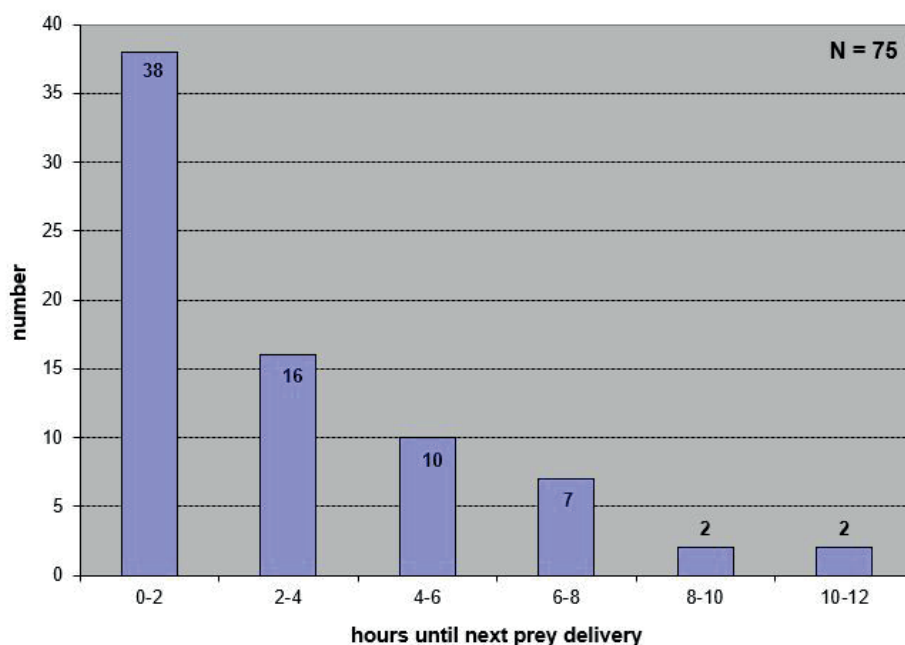


Figure 15 - Time elapsed between two consecutive prey deliveries in the following night (across the day time gap) during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 15 - Período de tempo entre duas entregas de presas consecutivas na noite seguinte durante o período de incubação num ninho de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, em 2015.

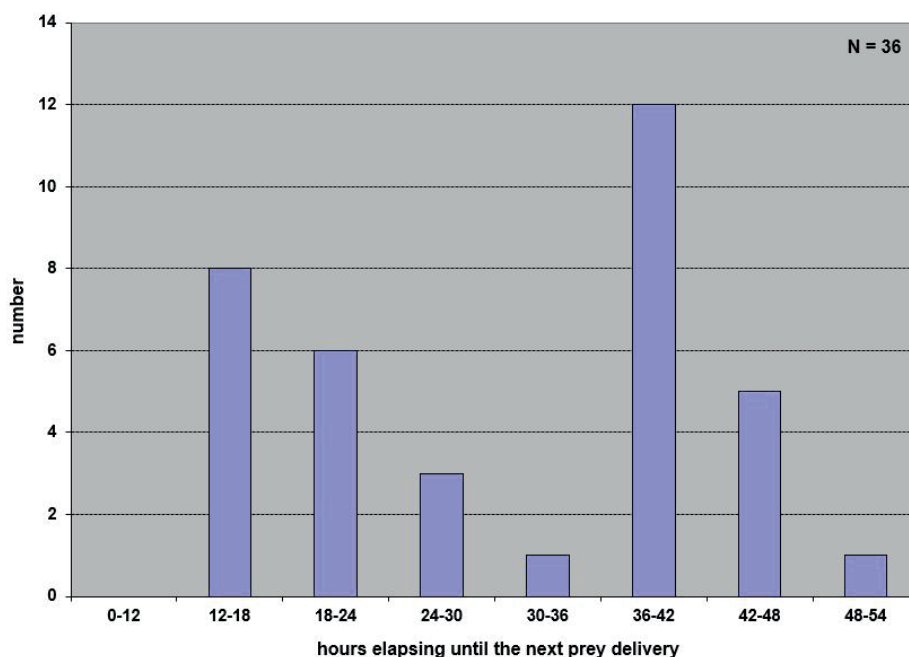


Table 6 - Prey deliveries during incubation and hatching periods at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

* means followed by different letters are significantly different (Tukey-Kramer test, $P < 0.05$; McDonald 2014)

Tabela 6 - Entrega de presas durante os períodos incubação e eclosão num ninho de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, em 2015.

	INCUBATION	HATCHING	INCUBATION & HATCHING
Period (date)	Feb. 22 - Mar. 26	Mar. 27 - Apr. 3	Feb. 22 - Apr. 3
Duration (calendar days)	33	8	41
Prey deliveries, number (%)	68 (61%)	43 (39%)	111
Prey deliveries, avg. per night \pm SD*	2.06 \pm 1.17 a	5.38 \pm 2.07 b	2.63 \pm 1.89
Min. / max.	0 / 4	3 / 9	0 / 9
Median	2	5.5	2

Hatching

Hatching and early brooding could not be observed because the female covered them. It was noted that the eggs had hatched after the female left the nest. During hatching the female half sat and half lay on the nest making a small space covered by long breast and belly feathers that both sheltered and hid the chicks. The female also bent her head low to groom, for feeding and cleaning the hidden chicks. Hence it was not possible to detect if the female assisted the hatching process or to quantify nestling care behaviour during the first days after hatching. Although there were no audio recordings it appeared that the female communicated with the chicks about 2 days before they hatched in response to their ‘beeping’ calls. No shell remains were visible in the hollow when she left the nest site, and she was also not observed to carry the shells in her beak when departing, as is common for many bird species. It is possible that the female crumbled and/or ate the shells for nutrition or to protect the hatchlings (sharp and/or a predator attractant).

Male Behaviour

In contrast to the courting period (Harms 2021a), the presence of the male Eagle-owl at the nest site was brief and totalled only

1:11:30 h for the incubation period. Of the male's 159 documented visits to the nest site, 111 represented prey deliveries to the female, and 37 were copulations or copulation attempts (see below). On average, each visit lasted 27 sec, ranging from 1-2 sec for the copulation attempts to over 2 min for some of the prey deliveries.

Prey deliveries

The male delivered prey 111 times (mean 2.7 per night, Fig. 11) and deliveries increased towards the end of the period and particularly during hatching. This change in behaviour was significant (1-way ANOVA with Tukey-Kramer test: $F_{1,39} = 37.4$, $P = 3.58 \times 10^{-7}$) with 68 (61%) deliveries occurring in the incubation period and 43 (39%) during the 8 day hatching period (Table 6). Approx. 70% of the prey deliveries lasted < 30 sec, and 90% lasted < 1 min. Prey deliveries occurred throughout the night but more frequently near dusk and dawn (Harms 2017a). The earliest first delivery occurred 6 min before sunset and 19 of 37 first deliveries were < 60 min after sunset (Figs. 12 & 13). Other deliveries occurred 2-11 h after sunset. The time of first prey delivery varied with a cluster of later first deliveries (7-26 March, Fig. 13) discussed below. In 38 of 75 consecutive deliveries (within the same night) the second occurred within 2 h (average time

Table 7 - Description of prey deliveries not accepted/eaten by a female Eurasian Eagle-owl (*Bubo bubo*) at a nest during the incubation period in Baden-Württemberg, Germany in 2015.

Tabela 7 - Descrição das entregas de presas não aceites/consumidas pela fêmea de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

DATE	TIME (START - END)	PREY	DESCRIPTION OF INCIDENCE
Feb 22	18:21:05 - 18:22:00	plucked bird; size: jay	Female (F) not present; Male (M) departed with prey
Feb 25	03:03:10 - 03:04:08	vole	M presented prey to F; F refused to accept; M put prey in front of F; vocalizations; M departed with prey
Feb 26	00:17:44 - 00:18:16	rat	F not present; M departed with prey
Feb 26	18:47:05 - 18:49:10	mouse	F not present; M swallowed prey before departing
Mar 12	03:20:37 - 03:22:48	plucked bird; size: blackbird	M repeatedly presented prey to F; F refused to accept prey; M departed with prey
Mar 22	00:46:30 - 00:48:15	not identifiable; size: rat or bigger	M repeatedly presented prey to F; F refused to accept; M put prey in front of F; intense vocalizations; M departed with prey

Figure 16 - Copulations (blue, in February) and copulation attempts (red, in March) during the incubation period at an Eurasian Eagle-owl (*Bubo bubo*) nest site in Baden-Württemberg, Germany in 2015.

Figura 16 - Cópulas (a azul, em fevereiro) e tentativas de cópula (a vermelho, em março) durante o período de incubação num local de nidificação de bufo-real (*Bubo bubo*) em Baden-Württemberg, Alemanha, in 2015.

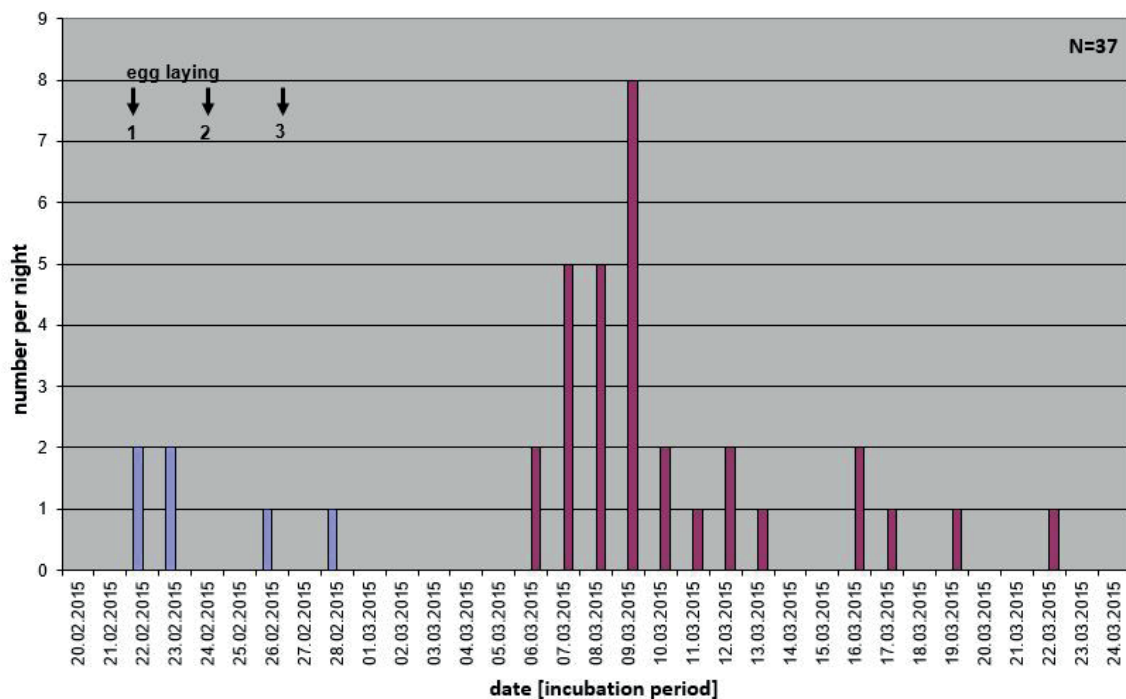


Table 8 - Percent frequency and percent estimated biomass of prey delivered by a male Eurasian Eagle-owl (*Bubo bubo*) during the incubation period to a nest in Baden-Württemberg, Germany in 2015.

Tabela 8 - Frequência e biomassa estimadas (em percentagem) das presas entregues pelo macho de bufo-real (*Bubo bubo*) num ninho em Baden-Württemberg, Alemanha, durante o período de incubação em 2015.

	N	% FREQUENCY	% BIOMASS
Mammals	77	69.4	69.8
mice (Muridae) and <i>Microtus</i> spp. voles	55	49.5	20.7
other voles (Arvicolinae)	18	16.2	33.3
rats (<i>Rattus norvegicus</i>)	3	2.7	12.0
ermine (<i>Mustela erminea</i>)	1	0.9	3.8
Birds (Aves)	11	9.9	21.6
Unidentified	23	20.7	8.7

2:49:46 \pm 2:33:59, range 4:43 min to 11:04 h, Fig. 14). There were four nights without prey deliveries (successive deliveries at least 36 h apart, Fig. 13). Eighteen of 36 (50%) successive deliveries spanning two successive nights were < 36 whereas 18 were > 48 hours (Fig. 15). For 44% of this period (18 of 41 d) the female waited > 36 h for a delivery.

Interactive behaviours

Principal male-female interactive behaviours quantified from video recordings during the incubation period were food transfers and copulations. Copulations during the incubation period may serve to maintain the pair bond whereas food exchanges are essential for successful incubation by the female.

Transfer of prey items

When the female became aware of the approaching male with prey, she usually faced him and stood up in a bowed position. The male landed and walked towards her. Prey were transferred immediately from beak to beak, sometimes with some tugging before the male released it. On several occasions, the male carried larger prey in his claws while landing, but immediately picked it up with

his beak to offer it to the female. Following transfer, the female crouched, turned her head and prey sideways away from the male and remained motionless for 5 to 20 sec. Her ear tufts were horizontal, and she looked up at the male. The male stood upright at the nest edge with erect ear tufts looking at her, then turned his head and body away before leaving. The male appeared to often utter intimate vocalizations (not recorded) after the transfer. The female usually maintained her bowed motionless posture until the male left. Small prey (mice or voles) were typically swallowed intact immediately soon after the male left. Larger prey was taken apart and consumed after she left the nest (see *feeding absences* above).

Copulations

Unexpectedly, starting on 6 March, 7 days after the last egg was laid, the male attempted to copulate 31 times over 17 days (Fig. 16).

Prey species frequency and biomass

Prey species

Small mammals (70%) were the most common of 111 prey delivered followed by birds (10%); 21% were not identifiable

because they were hidden from view or the video images were blurred (Table 8). Small mammals were mainly mice (Muridae; 66%) including voles (*Microtus* spp., *Arvicolinae* spp.). When unidentified prey was assumed to be small mammals (see methods) then their contribution to the estimated diet increases to 85% (frequency) and 63% (biomass) (Table 8).

Three bird carcasses were delivered within a short period of time; at 0:51:37, 1:08:09, and 5:10:16 on 19 March. In each case the female left immediately after accepting them returning after 4:06, 6:46 and 5:38 min, respectively. Nearly fledged nestlings of Carrion Crow, Rook (*Corvus frugilegus*), Common Kestrel (*Falco tinnunculus*) and Eurasian Buzzard were identified as prey remains from other Eagle-owl nests in this region (unpubl. data). It is possible, based on the timing of the bird prey delivered 19 March, that the male repeatedly returned to a nest to harvest nestling corvids which reproduce early in the area.

Prey mass

The total estimated biomass of 111 prey items delivered to the nest was 6,650 g. Six items were not transferred to the female (Table 7) and the total estimated biomass transferred to the female was 5,850 (average 143 g/night).

Discussion

This analysis of IR video recordings provides the first detailed evaluation of nest-site behaviours of a pair of Eagle-owls during incubation. The results confirm and detail previously reported behaviours, often derived from birds kept in captivity, and describe new behaviours.

Many bird species exhibit a variety of nest sanitation behaviours that reduce the likelihood of predation at the nest site (Van Tyne & Berger 1976). Likewise, the owls in this study were never observed to defecate at the nest site, a behaviour consistent with other

owl species (i.e., Mazur & James 2000). Presumably female owls have a strong need to defecate after each uninterrupted daytime incubation session which is required to protect the eggs from diurnal predators. The female Eagle-owl in this study left the nest to defecate at dusk (average absence duration $5:03 \pm 3:37$ min) when the risk of egg predation was reduced. Defecation outside the nest is also an opportunity for owls to mark their breeding territory using splashes of faeces as a visual signal to conspecifics (Penteriani & Delgado 2008).

Post egg laying copulations may be a common behaviour in some owl species. Video recordings at a Common Barn Owl (*Tyto alba*) nest box showed frequent copulations following prey deliveries through the incubation period and even after some of the chicks had emerged (unpubl. data). Continued copulations after egg-laying may be ritualized, i.e. reproductively non-relevant (Harms 2017b, 2021a) as evident from the tail positioning of the owls which indicated that cloacal contact was decreasing while copulation. Post laying copulations in barn owls have a food-reproduction context and may serve to strengthen the pair bond.

In contrast, the unsuccessful copulation attempts by the male Eagle-owl (Fig. 16) were associated with delayed food delivery (Fig. 13) and unlikely served to strengthen the pair bond. Moreover, new video recordings in 2018 and 2019 at two additional eagle owl nest sites showed no post-egg laying copulations (unpubl. data). The temporal distribution of the male's copulation attempts (Fig. 16) may reflect a decay curve after a surge of testosterone or another effector substance followed by its gradual degradation.

Female raptors, including owls, depend on the male's ability to provide prey during incubation and brooding to breed successfully (Newton 1979, Harms 2018a, 2019). The food requirements of Eagle-owls reported by Thiede (2003) differed from prey delivered in this study; average observed prey biomass transferred was ca. 60% of the afore-

mentioned daily requirements of the female during incubation. While not life-threatening it was unexpected and may have reflected a decreased local prey supply, the male's inability to provide sufficient prey, and/or the camera missing food transfers outside the nest site. The latter was unknown but anecdotally there was no evidence of this occurring during incubation. It was noteworthy that there was ample prey cached at the nest site during the subsequent chick rearing period (Harms 2019). Our knowledge of the food requirements of Eagle-owls and changes in prey availability under natural conditions is still very limited. The Eagle-owl, a diet generalist, is likely able to adapt to local or temporal shortages of preferred prey such as small rodents (Bezzel et al. 1976, Geidel 2014, Görner 2016, Leditznig 2005, Plass 2010, Lourenço 2006).

Thiede (2003) reported a 130 g stomach capacity for the Eagle-owl suggesting that multiple feedings are required to satisfy their daily dietary requirements. The capacity of the oesophagus to hold food may increase the amount of food an owl can ingest in a single feeding event, portions of which then gradually released into the digestive system. Contrasting with Thiede (2003), 14 field mice (with an estimated biomass of 280-340 g) have been found in the stomach of a female Eagle-owl (Görner 2016), and 17 *Microtus* skulls in a single pellet, thus suggesting a substantially greater holding capacity of the stomach than reported by Thiede (2003).

Video recordings of prey delivery and consumption are more accurate than that estimated by examining prey remains at nest sites or from pellets (Marchesi et al. 2002, Penteriani et al. 2005). Nielsen et al. (2015) used video recordings to examine food consumption of Eagle-owl chicks at a nest in Denmark. Numerous web camera recordings have been taken at Eagle-owl nests (i.e., www.uhu.webcam.pixtura.de) which represents a significant potential source of data that has yet to be published.

Avian prey were hard to identify from

grey-scale video recordings because of a lack of colour and their carcasses were delivered partially plucked, decapitated, and/or with no wings. Infrequently some diagnostic plumage or body features enabled the bird's identification (i.e., the unique feet of the Common Coot, *Fulica atra*).

A dependency on small rodent prey species has been reported for Eagle-owls in Europe (Bezzel et al. 1976, Geidel 2014, Görner 2016, Schweiger & Lipp 2011, and references in Harms 2018a) while European Rabbits (*Oryctolagus cuniculus*) were the owls' preferred prey in Mediterranean countries, often comprising over 90% of the diet (Donazar & Ceballos 1989, Lourenço 2006, Marchesi et al. 2002, Penteriani et al. 2005). Pellet-based diet studies are biased (Bezzel et al. 1976, Marchesi et al. 2002, Penteriani et al. 2005), often cannot distinguish the male and female's diets, and can be inappropriate or illegal regarding owl disturbance. Since prey remains are not left at the nest site during the incubation period, IR-video methodology appears to be the only approach to estimate details of the female's diet (prey species, mass and phenology).

In Denmark, rats (*Rattus norvegicus*) and hedgehogs (*Erinaceus europaeus*) were prominent prey consumed during the Eagle-owl chick rearing period revealed by video recordings (Nielsen et al. 2015), while mice played a minor role. Based on pellet analyses, Schweiger & Lipp (2011) determined voles (*Arvicolinae* spp.) were preferred prey during the Eagle-owl chick rearing period in Bavaria, Germany. Because of their diverse diet Eagle-owls are considered opportunistic hunters and generalist predators, but their diet is usually not a mirror image of the trophic diversity within their territory. Rather, they tend to exploit the most abundant food source available in their habitat (Bezzel et al. 1976, Donazar & Ceballos 1989, Görner 2016, Leditznig 2005, Plass 2010) and thus may be considered 'facultative specialists', in a regional context.

IR-video methods are valuable to study the

behaviour of difficult to observe nocturnal species such as Eagle-owls (Harms 2021b). Our knowledge of owl behaviour will grow if more studies use IR-cameras (van Harxen & Stroeken 2021, Kniprath 2018ab). Based on the video recordings made herein I was able to analyse the activities and behaviours of an incubating female and her mate during this important phase in their reproductive cycle. Likewise, pre-incubation and chick rearing behaviours at this nest site have also been analysed (Harms 2017a, 2019, 2021a). Analysis of behaviour from other owl nest webcams recordings should also be encouraged.

Note: Video clips showing selected scenes extracted from the recordings at the Eagle-owl nest site can be viewed on YouTube, channel "cth-ornitho" (www.youtube.com/channel/UCikFnM7cQEzDpCkM8gywvmQ). Additional information and published articles are available for viewing or download at www.researchgate.net/profile/Christian_Harms2/.

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