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Supplementary feeding improves breeding performance in Eurasian Eagle Owl (*Bubo bubo*)

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After more than a century of persecution and low reproduction rate, the Eagle Owl is extinct, scarce or still declining in many areas. One possible mitigating action is to supply them artificially with food, but earlier experiments with supplementary feeding of other species have produced varying effects. Supplementary feeding has some caveats and controversies and needs to be tested to avoid counterintuitive management outcomes. Here we present an experimental supplementary feeding trial on a wild population of Eagle Owls on two islands in the middle of Norway. An Eagle Owl population of 27 territories was investigated from 1999 to 2019, and supplementary feeding was provided in three territories over two to seven years. Other important factors for Eagle Owl reproduction that have changed during the 21 years were, in addition to supplementary feeding, included in the GLMM analyses. We found significant earlier egg-laying in territories with supplementary feeding, and a delay in egg-laying in periods with a high corvid population. The probability of producing young increased with supplementary feeding, but was negatively affected by an increased number of pedestrians. This experiment shows that supplementary feeding can enhance breeding performance in Eagle Owls, and that food availability is a limiting factor. Despite that, we would not recommend supplementary feeding as a general mitigating method to help Eagle Owls, because it is time-consuming, the fledglings will have problems surviving if there is not enough food available naturally in the surroundings, and predatory mammals can be attracted to the Eagle Owl territories.

1. Introduction

The provision of supplementary food has been widely used in the research on many species, and especially as a method to preserve endangered species. The effect of this artificial feeding depends on the ecology, limiting factors in breeding performance and survival of the actual species. Therefore, the outcome of supplementary feeding experiments has been successful, negative, or without detected effect. For example supplementary feeding in birds has resulted in fewer parasites, earlier egg-laying dates, and increased egg size, clutch size, fledging success and survival (Arcese & Smith 1988, Newton 1998, Robb *et al.* 2008, Siitari *et al.* 2015, Yang *et al.* 2016, Ferrer *et al.* 2018, Knutie 2019), some effects also including owl species like Ural Owl (*Strix uralensis*) (Brommer *et al.* 2004, Karell *et al.* 2007, Karell *et al.* 2008) and Tengmalm's Owl (*Aegolius funereus*) (Ilmonen *et al.* 1999). However, supplementary feeding has also increased aggression between individuals at the feeding stations, increased risk of pathogenic infections, higher nest predation in the surroundings, reduced clutch and brood size, reduced future reproduction, and biased chick sex ratio (Hipkiss *et al.* 2002, Oro *et al.* 2008, Robb *et al.* 2008, Cortes-Avizanda *et al.* 2009, Harrison *et al.* 2010, Peach *et al.* 2013, Plummer *et al.* 2013, Wilcoxen *et al.* 2015, Murray *et al.* 2016). Some feeding experiments did not show any clear changes in the investigated parameters (Gende & Willson 1997, Hörnfeldt *et al.* 2000, Genero *et al.* 2020). Despite many benefits of supplementary feeding, there are also some caveats and controversies (Cortes-Avizanda *et al.* 2016), and these experiences mean that the effects of feeding should be monitored and quantified when possible to avoid counterintuitive management outcomes.

After more than a century with a decline in the Eagle Owl population in Norway (Hagen 1952, Haftorn 1971, Penteriani & Delgado 2019), our population is estimated at 451–681 pairs (Øien *et al.* 2014). The Eagle Owl is classified as endangered (EN) on the Norwegian Red List (Kålås *et al.* 2015), and it is listed under Annex I of the European Union Birds Directive and Appendix II of the Bern Convention. The population is still declining in Norway (Øien *et al.* 2014), as in many other European countries (Penteriani & Delgado 2019). Mitigation action to save the species might therefore become necessary in some areas. Restocking is one possibility, but a previous project in Norway was not successful despite about 600 individuals being released (Penteriani & Delgado 2019). The effect of supplementary feeding has not been investigated on a wild population of Eagle Owls previously, as far as we know. We therefore present a supplementary feeding experiment carried out in Norway. If food is a limiting factor, we expect that both males and especially females will have better condition and can start egg-laying earlier. Earlier breeding is found in one supplementary feeding experiment with Ural Owls (Brommer *et al.* 2004), but not in another experiment (Karell *et al.* 2008). With parents in better condition, we also expect to find relatively more successful breeding attempts in fed territories compared with those that are unfed.

Food availability, however, is only one of many factors affecting the breeding ecology of Eagle Owls. We have therefore monitored times when some important changes have occurred in the different territories. Human disturbances have forced Eagle Owl from their breeding grounds, or led to poor reproduction (Jacobsen & Gjershaug 2014, Penteriani & Delgado 2019). We therefore expect that the Eagle Owl has better reproduction in those years and territories with fewer pedestrians nearby. Sheep might also be a problem because they may be present in Eagle Owl nesting sites in the spring and displace the owls from the nest site (Penteriani & Delgado 2019). According to this we expect better reproduction in the years and territories without sheep in late winter/spring. Mobbing behaviour from Hooded Crows (*Corvus corone*) and Ravens (*Corvus corax*) can be very intense both directly with physical attacks and indirectly by stealing food meant for the females or the chicks (Hagen 1952, Penteriani & Delgado 2019). Corvids are significant nest predators eating bird's eggs and chicks (Newton 1998, Husby 2019) and small mammals including lagomorphs (del Hoyo, Elliott & Christie 2009). This competition for common prey can, at least temporarily, reduce the number of available prey for the Eagle Owl when their chicks are growing and need food most (Newton 1998). Pictures taken by our surveillance cameras show both Crows and Ravens very close to Eagle Owls nests with eggs and small chicks. Despite the fact that Eagle Owl can catch and eat both Crows and Ravens (Hagen 1952), we expect to find a negative relationship between many crows and ravens and Eagle Owl breeding performance.

Along the western coast of Norway it is often windy and rainy, and the breeding cliffs should protect the breeding female from harsh weather. This is not always the case, and we have tried to improve some of the nesting sites by building a canopy and improve water drainage, and we expect that these nest site improvements will improve breeding performance. We lack data or data is too scarce on changes to analyse other important factors affecting Eagle Owl reproduction and survival such as power lines, wind farms, pesticides, pollutants and variation in prey populations (Penteriani & Delgado 2019).

To summarize, our objectives are to investigate how changes in different variables in the surroundings, including supplementary feeding, influence laying date and production of young in Eagle Owl, with the predictions given above.

2. Material and methods

2.1. Study area

Hitra and Frøya are the two island municipalities systematically investigated for occurrence of Eagle Owls at territory levels from 1999 to 2019. Hitra covers 755 km² and is connected to mainland Norway with a road tunnel of 5.7 km. Frøya has 241 km² and is connected to Hitra with a 5.3 km road tunnel. Both islands have few human inhabitants, with around 5,000 on each island. Hitra consists mostly of diorite and granite, with some gneiss and Devonian gravel. Most of the island is relatively flat, with its highest point at 345 m above sea level, but the terrain is commonly broken with steep cliffs. The island has many spruce and pine forests, mires and a few farmland areas along the coast where most of the Eagle Owls are breeding. Frøya is made of gneiss and granite, with 95% of the land area less than 60 m above sea level and the highest point 76 m above sea level. This island is mostly without trees, but has a few conifer plantations and a few farmland areas (snl.no). Mink (*Mustela vison*) and Common Otter (*Lutra lutra*) are the main mammal predators on the islands, but Brown Rat (*Rattus norvegicus*) and European Hedgehog (*Erinaceus europaeus*) can also be predators on bird's nests and chicks.

Some Eagle owl territories on Hitra and Frøya are abandoned, and new territories have been found based on information from people, listening for vocalization in the field, and nest searching. From 2015 we used Wildlife Acoustic Sound Meters (SM 2+ and SM 4) year round, which increases the probability of detecting the Eagle Owl vocalization (Andreychev *et al.* 2017). Nests are mainly controlled in June (May–July) for nestling production, with only one person at the nest and preferably during the night to avoid detection from corvids, gulls, White-tailed Eagles (*Haliaeetus albicilla*) which are common on both islands, and humans. Of the 27 different territories we have data from, 15 have been investigated in all of the 21 years including the years after the territory was abandoned, while 12 territories have been found later. Of the territories found later, three have been investigated for between 15 and 19 years, while the nine others have been found less than 10 years ago. Most of these new territories are mainly re-established or newly established pairs. The number of territories are 18 on Hitra and 9 on Frøya, of which a mean of 8.9 (range: 6–13) and 4.0 (range: 2–6) have been occupied each year on the two islands respectively.

Eagle Owls feed on a wide variety of prey on the islands (Obuch & Bangjord 2016). Birds, especially gulls, are the most important prey both in numbers and mass, but the Eagle Owls have also taken a substantial number of ducks and waders, corvids, thrushes and smaller numbers of other bird species. Mammals are less widespread prey, and the Mountain Hare (*Lepus timidus*), Brown Rat and European Hedgehog are most important. Voles (*Microtus agrestis)* are rare and Lemmings (*Lemmus lemmus*) are absent, and small mammals have only minor variation in numbers from year to year and do not have large cyclic changes in populations as they have in other areas. This makes our investigation area well suited for supplementary feeding experiments of Eagle Owls, as fluctuations in the abundance of small rodents strongly affect Eagle Owl occurrence (Penteriani & Delgado 2019). Some Eagle Owls take a large number of Common Frogs (*Rana temporaria*), but their total mass is small. Unfortunately, we do not have sufficient data about the occurrence or change in abundance of the most important prey on these two islands during the investigation period, but the most important prey species are gulls, which typically do not show cyclic population fluctuations.

2.1. Supplementary feeding

Three territories got supplementary feeding for seven (2013–2019, Hitra), five (2014–2017, 2019, Frøya) and two (2018–2019, Hitra) years respectively. The two territories on Hitra are neighbouring territories, with 2.5 km between the nest sites. The amount of supplementary food varied according to season and number of birds in the family, and their age. The food delivery strategy varied somewhat between the territories, from about 1–3 times per week before egg-laying, and gradually increasing to 2–7 times per week when nestlings grew up and stayed in the territory, and with reduced feeding after the young had left the territory. In a similar way the amount of food delivered daily varied throughout the year from one Hooded Crow (about 500 g) before egg-laying to most often 1–2 kg (maximum 2.5 kg) during the nestling period. The first mentioned territory received food all year round, while there were some breaks in the other two, especially during late autumn and winter. The expected needs for Eagle Owls are 400 g per day per adult in January–April, and about 300 g per day in May–August, and each young might consume about 500 g per day in May–August (Penteriani & Delgado 2019). We have normally given less food than the anticipated needs, and only about half of the needs of the adults if they were fed outside the breeding season.

In a fourth locality additional food was offered only for ten days because one White-tailed Eagle found the feeding place and took the food, even when the feeding place was moved. This territory is not included as a territory with supplementary feeding in our analyses. White-tailed Eagles are normally only day active, but here they can be active during the night because it never gets really dark in our northern areas during the summer.

The breeding status of the Eagle Owls was well known in the chosen territories, and frequent food delivery was possible without being detected by other people. The food was delivered in open places 300–600 meters away from the Eagle Owl nests, but close to commonly used roosting places, and mainly after sunset to avoid competition from most scavengers. Cameras with MMS function were placed both at the feeding place and at the nest. The food was of high quality, such as killed crows, rabbits and cocks, fresh road-killed *Cervidae*, and Atlantic Salmon (*Salmo salar*) approved for humans.

2.2. Dependent (target) variables

We have analysed two dependent variables that can inform us about the breeding performance: Date when the first egg was laid, and if the territory produced fledglings or not. Fledgling is here defined as the age when the young was ringed.

The date when the first egg was laid was either determined by camera surveillance (n = 7), or estimated from the size of the young when it was ringed by judging the age of the young (Penteriani *et al.* 2005), minus 35 days brooding time and taking into consideration that brooding starts from the first egg (del Hoyo *et al.* 1999) (n = 80). In the five nests where we knew both the exact laying date and estimated the age of the young, the differences were from zero to only a few days, both sooner and later. Day 1 is 1 January, day 2 is 2 January and so forth, and leap years were taken into consideration in the day numbers.

No fledglings produced was categorized as 1, and at least one fledgling produced was categorized as 2. We planned to use 'number of fledglings' as dependent variable instead of 'fledglings produced or not', but there were not enough data for some categories to run this analysis properly.

2.3. Independent variables (Fixed factors)

All independent variables are categorized. Experimental supplementary feeding is composed of territories with no feeding, that is the normal situation (category 1), and territories with supplementary feeding (2). Change in number of pedestrians, directly observed or indirectly seen from preparation of new tracks, the trampled vegetation on and near the tracks, are categorized as less than normal (1), normal; that is the same level as the first year the territory was included in the analyses (2), and increased activity compared to normal (3). In practice, a pedestrian is not always only a human, but also with dogs that are not necessarily close to the owner on a leash all the time. The number of roads were categorized as no change (1) or more roads (2), since fewer roads was not an option. These independent variables were judged within 2 km from the nest site. In addition, we added whether the nest cup was natural (1) or artificially improved (2), and whether sheep used the territory (2), or not (1), prior to egg-laying. Included in the independent variables are also island Hitra and Frøya with category 1 and 2 respectively.

In 2011 and 2013 a program was started to reduce the number of Crows and Ravens on Hitra and Frøya respectively. About 100 birds of each species were killed yearly in 2011 and 2012, and increased to1006.6 ± 22.9 SE and 189.4 ± 22.5 SE for Hooded Crows and Ravens respectively for 2013–2019. As Crows and Ravens move around on and between the two islands quickly and easily, a reduction in number of corvids in a few areas probably influences the numbers in the whole area. We included a variable called corvid population that was categorized as 1 before the program was presumed to be effective (1999–2013), and categorized as 2 afterwards (2014–2019), and identical for all territories. We presume that the number of corvids have increased on both island from 1999 up to when the reduction program started because they have got more available food from open refuse tips, remnants after the hunting of Red Deer (*Cervus elaphus*) and European Roe Deer (*Capreolus capreolus*), a change to having sheep outside the whole year with carcasses left for scavengers, and generally milder winters with less snow. We have no details about the change in corvid populations, and we therefore categorize the number of corvids only according to the predator control program.

2.4. Statistics

Generalized linear mixed effect models (GLMMs) are powerful tools that has increased in popularity the last decade (Harrison *et al.* 2018). GLMM can estimate independent and random effects in one model, and yield efficient estimators even for unbalanced designs which is a great advantage because data are often unbalanced (SPSS 2005). GLMM removes variability in responses that are associated with random factors rather than the conditions of experimental interest, thus reducing Type I error rate (Lo & Andrews 2015). All the statistical analyses were performed with SPSS (IBM Statistics SPSS v. 27).

For the dependent variable date of laying the first egg, we developed a global model including all potentially relevant effects on breeding performance we had information about (Burnham & Anderson 2002). We knew the date of the first egg in only 87 cases of 405 possible (14–27 territories investigated yearly during the 21 years). For these territories, some independent variables had very little data for some of the categories. When we used Akaike's Information Criterion (AIC_C) to find the best model (Burnham & Anderson 2002), the model including island (52 territories/years on Hitra and 35 on Frøya), corvid population (29 low and 58 high), pedestrians (9 fewer, 64 normal, 14 more) and supplementary feeding (77 without feeding and 10 with feeding) as independent variables gave the best result. Other models gave higher AIC_C values, mostly with $\Delta AIC\ \ > 20$ compared with the best one, which give them no support (Burnham & Anderson 2002). We wanted to use territory number and year as random factors in both analyses, but that was possible only with production of young or not as a dependent variable. For date of egg-laying as dependent variable, we could only use year as a random factor, because territory number alone or together with year made the final Hessian matrix non-positive. However, the results with year only, or the other variants including territory number as random factor created nearly the same results. Here we only included the analysis with year as a random factor when we analysed the effects on laying date.

In the analysis with laying date as dependent variable, the correlations between the four independent variables we used were far below the suggested limit of 0.7 (Dormann *et al.* 2013). The Variance Inflation Factor (VIF) values, independent of which of the independent variables we selected as dependent variable, were always less than 2 in all used analyses. This is within a stringent recommendation (Burnham & Anderson 2002, Zuur *et al.* 2010). Using graphical tools (Zuur *et al.* 2010), the histogram with Regression Standardized Residuals and Frequency showed normal distribution (Lo & Andrews 2015), and Scatterplot between Regression Standardized Predicted Value and Regression Standardized Residuals confirmed linearity of the model with a horizontal regression line through zero. R^2 was 0.61, and SE of the estimate was 8.6, informing about variation explained and residual variation of the independent variables, respectively. The data in this model seems to have a constant error variance (homoscedasticity) and no overdispersion (Burnham & Anderson 2002). The ANOVA of the model gave $p < 0.001$, indicating that at least one of the four independent variables have significant effect on the dependent variable. The random effect of year was not significant (*Z* = 0.138, *p* = 0.890). The corrected model, with normal probability distribution and link function identity, was significant ($F_{5,81} = 20.99$, $p < 0.0005$).

When we analysed production of fledglings or not as a dependent variable, we used only territories investigated for more than 10 years (n = 347 cases). That is because all independent variables were changes over time, and longer time series are therefore preferred. The global model included a priori all the independent variables, but AIC_C analyses included island (208 and 139 cases on Hitra and Frøya respectively), pedestrians (12 fewer, 195 normal and 140 more) and supplementary feeding (335 with no feeding and 12 with feeding) in a good model. The model was a bit better with changes in roads and corvids included, but they gave individually far from significant results and $\Delta AIC < 5$ compared with the model above. That make it possible to reduce the number of variables in the model (Burnham & Andersen 2002), as recommended (Harrison e*t al.* 2018). Tests of this model gave $R^2 = 0.16$ and SE of Estimate = 0.36, and the ANOVA test of the model was significant (*F* = 21.66, $p < 0.001$). The random effects of year (*Z* = 0.670, *p* = 0.503) and territory number (*Z* = 0.608, *p* = 0.543) were not significant. With production of young to fledging or not as a dependent variable, the corrected model, with binomial distribution and link function logit, was significant ($F_{4,342} = 12.78$, $p < 0.001$).

We also compared whether the number of young produced to fledging stage differed between territories with and without supplementary feeding, both before and after the feeding started, with the non-parametric Mann–Whitney *U*-tests. In these tests we included all territories with Eagle Owls present, and in additional tests only territories investigated for more than 10 years. We used the raw data in figures illustrating the relationship between dependent and independent variables.

3. Results

3.1. Laying date of the first egg

Laying date of the first egg was registered 87 times during the research period. In territories with supplementary feeding the eggs were laid significantly earlier than in territories without supplementary feeding, and the first egg was laid later in periods with a high corvid population (Table 1, Figs. 1 and 2). These two independent variables were the only ones that significantly influenced the laying date in the GLMM analysis. In one territory with supplementary feeding, one of the years more than 40 young White-tailed Eagles roosted regularly from February to April on the same cliffs as the Eagle Owl nest, and the laying date of the first egg was postponed by 62 days (to day 121) compared with the two closest years before (day 56 and 57), and after (day 65 and 58). As this disturbance was a natural phenomenon, the year with this strong disturbance was included in the analysis (Table 1), but it resulted in a much higher CI than normal (Fig. 1). This pair of Eagle Owls received supplementary feeding during this whole period without competition for the food from White-tailed Eagles.

Table 1. GLMM analysis with date of the first egg as dependent variable (n=87), and the independent variables listed. All independent variables, with category value given in brackets, are compared with the lowest category value.

Model Term	Coefficient	SE	*t*	*p*	CI_{lower}	CI_{Upper}
Intercept	–17.1	223	–0.077	0.939	–460.7	427
Island (Frøya)	–2.1	2.0	–1.034	0.304	–6.1	1.9
Corvid population (higher)	12.5	2.6	4.841	**< 0.001**	7.4	17.7
Pedestrians (normal)	4.4	3.4	1.316	0.192	–2.3	11.1
Pedestrians (more)	6.1	4.0	1.543	0.127	–1.8	14.0
Supplementary feeding (yes)	–20.7	3.4	–6.139	**< 0.001**	–27.5	–14.0

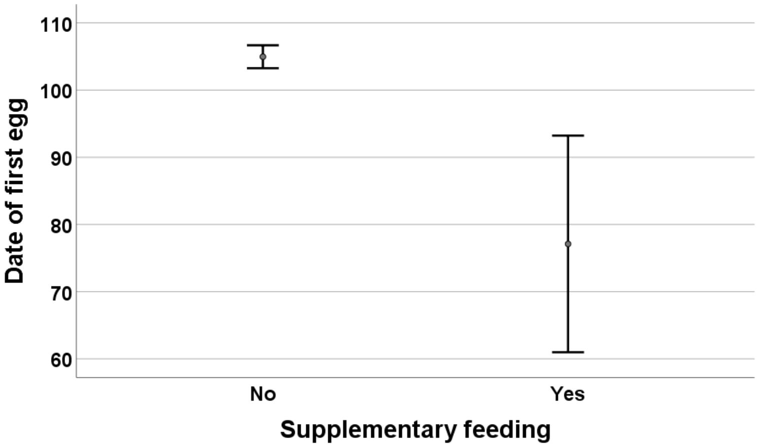

Fig. 1. Date of the first egg (± 95% CI) without and with supplementary feeding (n = 87).

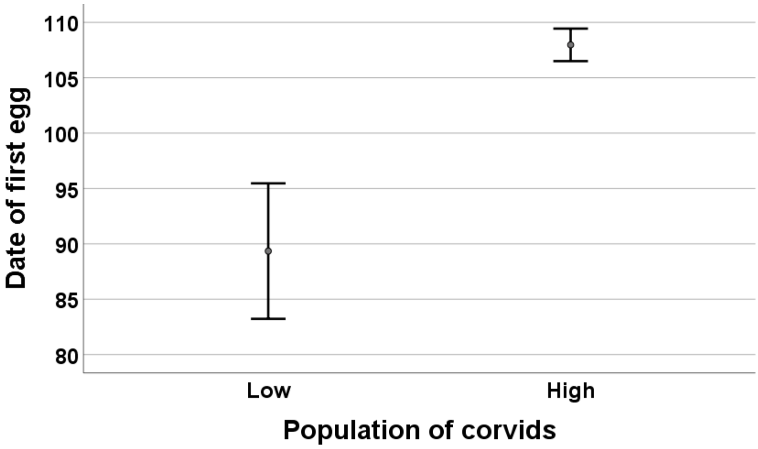

Fig. 2. Date of the first egg (± 95% CI) with low and high corvid population (n = 87).

3.2. Production of young to fledging stage

The GLMM analysis of the independent variables influencing production of young or not, shows some differences between the two islands (Table 2). In addition, more pedestrians decreased the probability of raising young (Table 2, Fig. 3). Supplementary feeding increased the probability of raising fledglings (Table 2, Fig. 4). Changes in number of roads, sheep and attempts to improve the nest cup quality did not show significant effects on the probability of producing fledglings.

Before supplementary feeding started in 2013, there were no significant differences in the number of young raised to fledging stage between territories without and with extra food (Mann–Whitney *U*-test: $Z_{\mathrm{n}\,=\,139\text{ and }25} = -0.652$, $p = 0.514$), but the difference was significant after feeding started ($Z_{85,\,19} = -2.171$, $p = 0.030$).

Territories without extra feeding had similar production of young before the feeding experiment started compared with after ($Z_{139,\,85} = -0.270$, $p = 0.787$), while the experimental group increased the production of fledglings ($Z_{25,\,19} = -2.265$, $p = 0.023$).

These results include all territories with Eagle Owl present. By including only territories used more than ten years, and not the territories established later than 2010 or that have been controlled less than ten years, the results of the statistical tests were similar (not presented).

Table 2. GLMM analysis of production of young (no chicks or at least one chick survived until fledging) as target variable, and the independent variables listed. All independent variables, with category value given in brackets, are compared with the lowest category value.

Model Term	Coefficient	SE	*t*	*p*	CI_{lower}	CI_{Upper}
Intercept	261.6	60.9	4.296	**< 0.001**	141.8	381.4
Island (Frøya)	1.8	0.6	2.780	**0.006**	0.5	3.0
Pedestrians (normal)	–3.5	0.8	–4.418	**< 0.001**	–5.0	–1.9
Pedestrians (more)	–4.7	0.9	–5.423	**< 0.001**	–6.4	–3.0
Supplementary feeding (yes)	3.9	0.8	4.961	**< 0.001**	2.4	5.5

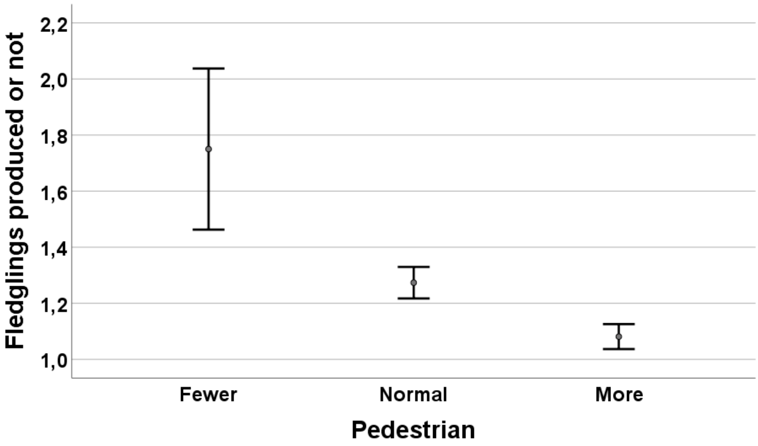

Fig. 3. Fledglings not produced (category 1) or fledglings produced (category 2) (± 95% CI) in relation to changes in number of pedestrians in the territory within 2 km from the Eagle Owl nest, with normal level describing the level in the first year (n = 347).

4. Discussion

It is well known that Eagle Owls can eat carcasses (Penteriani & Delgado 2019), and we saw on our wildlife cameras that the Eagle Owl came and took the food that we delivered. Therefore, the food delivery reached the Eagle Owl as our target species, a needed condition to measure the effects of supplementary feeding. The Eagle Owl territories in our investigation area are quite stable, with mostly the same male and female in them both before and during feeding periods shown by DNA analyses. The only exception is in one territory with several unsuccessful breeding attempts in years without supplementary feeding, and when supplementary feeding started the male was alone for two years before the neighbouring female settled the third year. Therefore, the improvements in breeding performance in general are not caused by higher ranked birds invading the territory (Aparicio & Bonal 2002), but because the ones living there improved their ability to lay eggs earlier and raise young to fledging stage.

4.1. Laying date of the first egg

We found more than 25 days earlier egg-laying by Eagle Owls in territories when they received extra food. Earlier egg-laying after supplementary feeding is common, also in experiments with large owls like the Ural Owl (Brommer *et al.* 2004), but not always (Karell *et al.* 2008). The effect we found is surprisingly strong as the advance of laying date normally decreases with higher latitude (Schoech & Hahn 2008). Earlier laying in fed broods is

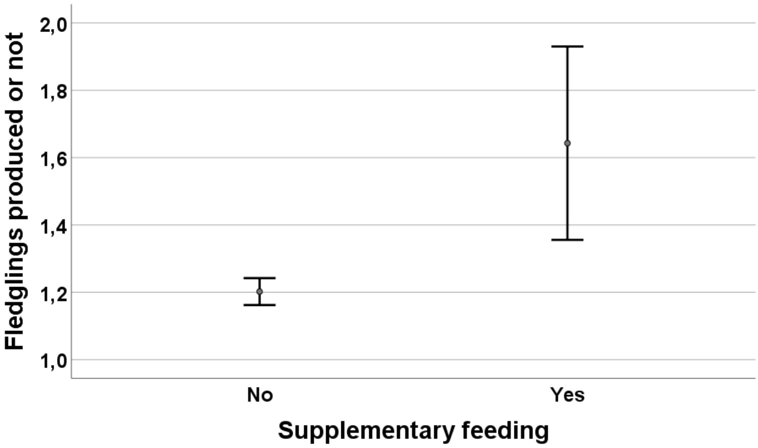

Fig. 4. Fledglings not produced (category 1) or fledglings produced (category 2) (± 95% CI) in relation to supplementary feeding of the Eagle Owl in the territory (n = 347).

consistent with our predictions. Early egg-laying means early fledging, which is advantageous because the young will have a longer period with good food conditions on the islands before some of the gull species leave the area in the autumn, and because it reduces the exposure to the detrimental blood-sucking black flies (Diptera, *Simuliidae*) (Malmquist *et al.* 2004) in the nest (Karell *et al.* 2009). Both Black flies and *Ceratopogonidae* can be numerous on the chicks in some Eagle Owl nests on Hitra and Frøya, especially on late hatched nestlings (own observations).

The laying date was significantly later in periods with many Crows and Ravens on the islands. The two most plausible reasons for this are: 1) Eagle Owls are stressed by the large number of corvids (Hagen 1952), and perhaps use more energy and delay egg-laying or 2) Eagle Owls are in better condition caused by increased prey abundance after corvid removal, and lay the eggs earlier. During the autumn, many corvids come to the islands because the food availability is better here on the coast than in harsher winter environments inland. Crows and Ravens are migratory (Cramp & Perrins 1994; del Hoyo *et al.* 2009), and may come from very distant areas (Sweden, Finland and Russia) to spend the winter in Norway (Overskaug & Sørensen 1984). Many of the corvids killed since 2013 were probably mostly wintering birds from other areas together with some local corvids (Overskaug & Sørensen 1984). Important prey species for Eagle Owl are found to increase, especially the post breeding numbers, in some predator removal experiments (Madden *et al.* 2015, Aebischer *et al.* 2016; Roos *et al.* 2018; Kämmerle & Storch 2019), but not in all (Madden *et al.* 2015). In areas with both mammalian and avian predators, the effects of removal of one or a few predators can be replaced by increased predation by others (Ellis *et al.* 2020). However, the most common mammalian nest predators on the mainland are absent on Hitra and Frøya. In late winter most Crows and Ravens leave Hitra and Frøya, and we found no significant effect of corvids on the production of Eagle Owl young which should be expected if increased prey abundance after corvid removal was the main reason for earlier egg-laying in periods with fewer corvids (Table 2). However, we cannot ignore the possibility that the re-established and new territories the last years are made possible by a reduction in the number of corvids.

4.2. Production of young to fledging stage

Increased numbers of pedestrians reduced the probability that Eagle Owl fledglings were produced (Table 2, Fig. 3). Long-term persecution of Eagle Owls in the whole of Europe resulted in extinction of several breeding populations, and the species also suffer from many other threats (Penteriani & Delgado 2019). It is known that Eagle Owls are extremely sensitive to human disturbance, which may cause parents to abandon eggs and even small young (del Hoyo *et al.* 1999). The female never lays a replacement clutch if she deserts the nest following a disturbance during or immediately after hatching (Penteriani & Delgado 2019). The negative effect of increased number of pedestrians in the Eagle Owl territories is in accordance with our prediction. On Hitra and Frøya the number of pedestrians in the terrain is normally sparse during the winter, that is before Eagle Owl lay their eggs, but increases several-fold during the spring and early summer when Eagle Owl raise their young. That might explain why change in number of pedestrians from year to year did not influence laying date but had a significant effect on production of fledglings.

Despite the negative effect of pedestrians, who are most active during daytime, Eagle Owls often hunt near human settlements at night without a reduction in production (Marchesi *et al.* 2002). Here they find both rats and gulls, which are included in the Eagle Owl diet both on Hitra and Frøya (Obuch & Bangjord 2016). Hunting near urban areas might cause other problems for the Eagle Owl and other raptors, such as increased levels of anticoagulant rodenticides (Lopez-Perea *et al.* 2019), and this and other toxins have been found at high levels in dead Eagle Owls in Norway including Hitra and Frøya (Bernhoft *et al.* 2018).

Supplementary feeding increased the probability that Eagle Owls produced fledglings (Table 2, Fig. 4). The importance of a decrease in prey availability has for decades been mentioned as a possible explanation of Eagle Owl occurrence and breeding performance (Hagen 1952, Fremming 1986), and it is now considered to be especially important as the volume of other threats are increasing (Penteriani & Delgado 2019). However, this is the first experimentally evidence showing that more food significantly improves breeding performance in Eagle Owls, in support of our prediction. Also in other owl species, supplementary feeding increased reproductive output (Haley & Rosenberg 2013, Jacobsen *et al.* 2016), and/or reduced the costs of caring for their current offspring (Brommer *et al.* 2004, Karell *et al.* 2007, Eldegard & Sonerud 2010, Jacobsen *et al.* 2016). In both Tengmalm's owl and Ural Owl, breeding females suffered less from blood parasites in years with high vole abundance and in years with supplementary feeding, and females with infection were in poorer condition than uninfected females (Ilmonen *et al.* 1999, Karell *et al.*2007). In Ural Owl the positive effects of supplementary feeding even lasted to the following breeding season, as the females still had fewer parasites and laid larger clutches than control females (Brommer *et al.* 2004, Karell *et al.* 2007).

Supplementary feeding seems to be most valuable as a buffer during periods of low natural resource availability during the breeding cycle (Maggs *et al.* 2019) or in periods of the year when food availability is limited compared to the needs (Siriwardena *et al.* 2007). In addition, poorer territories should be given priority where the reproductive rate has the potential of being raised most (Byholm & Kekkonen 2008, Rooney *et al.* 2015, Ferrer *et al.* 2018). Effects of extra food might therefore vary from year to year and when during the year depending on the availability of natural prey (Dewey & Kennedy 2001, Karell *et al.* 2007, Siriwardena *et al.* 2007).

We found that the number of young raised to fledging stage was similar in territories without supplementary feeding before and after the feeding started, and similar to the territories with feeding before the feeding started. After feeding started, the territories with feeding increased their production of young compared both with the period before feeding and with the control group without feeding. These results imply that there were no general improvements influencing the production of fledglings in the actual territories on the two islands that can explain the improvements in the territories with supplementary feeding.

The lack of significant effects of changes in number of sheep and roads in the territories and artificial improvement of the nest was not in accordance with our predictions. That might be a result of too little data, and that the results were not consistent enough to give significance. The probability to produce fledglings was different between the islands, which might be expected due to the differences between them (Chapter 2.1).

4.3. Conclusion

The positive effects of supplementary feeding show that food availability is a limiting factor in some territories in the investigated area. This is in accordance with the conclusions in supplementary feeding experiment with other bird species (Brommer *et al.* 2004, Von Post *et al.* 2013, Peach *et al.* 2018). Food availability is found to be among the most important factors influencing fluctuations in Eagle Owl population density (Penteriani & Delgado 2019).

In general, supplementary feeding of Eagle Owls is time consuming, and connected to competition disturbance from other meat eating birds and mammals. In addition, it is in most situations useless as a mitigating action when the hunting grounds used by Eagle Owls are destroyed e.g. for industrial purposes. That will make it necessary to continue with the feeding effort for many years, and the independent young birds will have great problems to find enough food to survive the first years and later reproduce in a landscape with little natural prey. Supplementary food for an endangered falcon species increased the short-term survival and reproduction, but not in the long-term, since there was little available food in the area (Sweikert & Phillips 2015). The best practice is to preserve a rich and varied wildlife in the Eagle Owl territories, and of course avoid all the infrastructure, disturbances, poisoning and other factors that are known to be detrimental for Eagle Owls. If Eagle Owls are in danger of becoming extinct in an area, well planned supplementary feeding can be helpful until other mitigation actions are operative. If the resources available for supplementary feeding are limited or year round feeding is not feasible, it is important to take into consideration when during the year/breeding cycle the extra food is most effective (Brommer *et al.* 2004, Siriwardena *et al.* 2007, Maggs *et al.* 2019). If so, we recommend to start feeding before egg-laying, and continue to the chicks leave the territory with a gradual reduction before feeding is ended.

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Lisäruokinta parantaa huuhkajan lisääntymismenestystä

Huuhkaja on monilla alueilla harvinainen tai vähenevä laji, johtuen vuosikymmenien vainoista ja alhaisesta lisääntymismenestyksestä. Lisäruokinnalla voidaan mahdollisesti kasvattaa kantaa, mutta aiemmat lisäruokintakokeet ovat tuottaneet vaihtelevia tuloksia. Lisäruokinnalla voi olla myös haittavaikutuksia, joten sen haasteita pitäisikin selvittää paremmin. Raportoimme tuloksia huuhkajien lisäruokintakokeilusta, joka toteutettiin Keski-Norjassa kahdella saarella. 27 huuhkajareviiriä seurattiin 1999–2019, ja lisäruokintaa suoritettiin kolmella reviirillä seitsemän vuoden ajan. Analyysiin sisällytettiin myös muita huuhkajan pesintään vaikuttavia ympäristötekijöitä, jotka ovat muuttuneet tutkimusjakson aikana. Havaitsimme, että lisäruokinta aikaisti huuhkajien pesintää. Korkeat varislintutiheydet taas myöhäistivät pesintää. Lisäruokinta nosti pesinnän onnistumisen todennäköisyyttä, kun taas ihmisistä johtuva häirintä vähensi pesinnän todennäköisyyttä. Kokeemme osoittaa, että lisäruokinta voi lisätä huuhkajan lisääntymismenestystä, ja että ravinnon saatavuus on menestystä rajoittava tekijä. Emme kuitenkaan suosittele laajamittaista lisäruokintaa, koska se on aikaa vievää ja voi houkuttaa petoja, ja koska poikasien menestys voi olla heikko, jos luonnollista ravintoa ei ole riittävästi tarjolla.

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