Limitations of Owl Reproduction in the Wild: is there a Role for Food Quality Besides Quantity?

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Limitations of owl reproduction in the wild: is there a role for food quality besides quantity?

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Avian studies have shown that food quality (amino acid load) can act as a limiting factor in reproduction and possibly breeding density. In owls, the role of food quality may have been largely overlooked due to the strong effect of food quantity. I examined evidence of food quality limitation in owl reproduction from four sets of data: (1) population data in Tawny Owls and diurnal birds of prey in a degenerate forest, (2) post-laying breast muscle conditions of Tawny Owls *Strix aluco* and Sparrowhawks *Accipiter nisus* which strongly relied on internal amino acid stores during egg formation, (3) amino acid deficiency-related embryo anomaly data in failed eggs of Barn Owls *Tyto alba*, Little Owls *Athene noctua*, and two reference species, and (4) growth of Tawny Owl chicks experimentally fed with day-old chickens or mice. The Tawny Owl population was found to be stable whereas sympatric bird of prey species greatly declined; breeding female Tawny Owls (n = 5) did not show a decline of breast muscle tissue as was found in Sparrowhawks. Embryo mortality from amino acid deficiency was estimated at 63% and 12% in Barn Owls and Little Owls, respectively. Growth rate of Tawny Owl chicks did not relate to food type. I conclude that egg amino acid investments can affect embryo viability in owls, but mainly in relation to reproductive strategy instead of environment. I hypothesize that owls can obtain additional amino acids from their caecal bacteria, which are lacking in birds of prey, and thereby are less dependent on amino acid availability in the food chain to acquire the amino acids needed for egg formation and chick growth.

Key words: forest degeneration, Tawny Owl, *Strix aluco*, diet, food quality, reproduction, amino acids, egg failure, Barn Owl, *Tyto alba*, Little Owl, *Athene noctua*

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INTRODUCTION

Most owl species respond to elevated local food availability, either by an increase in breeding pair numbers (Korpimäki 1992, Village 1987, Wiklund & Stigh 1986) or the production of larger clutches, resulting in more offspring (Baudvin 1986, Petty 1987, Schönn *et al.* 1991, Taylor 1994, de Jong 2006). In poor years or habitats, the scarcity of food often limits clutch size and breeding success. In bird taxa as diurnal birds of prey food quality (especially in terms of micronutrient load) has been identified as an additional limiting factor for reproduction and possibly breeding density (Selman & Houston 1996, Ramsay & Houston 1998, van den Burg 2000). This paper focuses on the question of whether owl reproduction can be similarly reduced by food quality as has been found in raptors. Due to the strong effect of food quantity, the role of food quality may have been largely overlooked in owls.

The forest soil in my central Netherlands study area is poor in nutrients: it is sandy, acidic, and has been depleted of minerals by excessive agricultural use (top soil removal) during recent centuries. This activity has caused heathlands to develop into drift sands, which were later largely reforested. The numbers of raptors (i.e. Eurasian Sparrowhawk *Accipiter nisus*, Northern

Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, Hobby *Falco subbuteo*, Common Kestrel *Falco tinnunculus*) fell sharply during the 1990s (van den Burg 2002). Detailed studies on Sparrowhawks showed a correlation between egg failure and egg amino acid investments (unpubl. data). Lack of amino acids in the avian diet can be compensated for by parental investments from the breast muscle (Houston *et al.* 1995). Nowadays, the decline of breast muscle condition during egg-laying in Sparrowhawks is extreme (similar to starving birds in winter), which indicates that amino acids are limiting egg production (and subsequent hatching success). I expect that only female Sparrowhawks capable of delivering large nutrient investments from their own bodies into their eggs are now able to breed successfully in my study area.

The precise reason for these changes in the bird community is still the subject of study and speculation. The forests in my study area are largely degenerated due to soil acidification (for effects on birds see Graveland & van Gijzen 1994, Graveland *et al.* 1994) from past and ongoing nitrogen deposition. High nitrogen deposition has been shown to disturb the mineral and amino acid balance of deciduous plants and trees (Pérez-Soba 1995); in forests that are very poor in other sources of nitrogen, the strongest effects may be expected. Because animals are unable to synthesize about 10 amino acids themselves (Chapman 1998), an imbalance of amino acids that arises in the vegetation may act through the entire food chain. Whereas the detrimental effects of acidification on trees during the 1970s and 1980s were direct and severe, the effects of nitrogen deposition were at first most likely reduced by altered plant growth (e.g. grass encroachment), taking much of the excess nitrogen from the forest ecosystem.

To study whether owls can be affected by amino acid imbalances, I investigated whether (1) the Tawny Owl *Strix aluco* population in my study area has, similar to diurnal birds of prey, declined from the early 1990s until now, (2) Tawny Owls show reduced breast muscle conditions, similar to Sparrowhawks, (3) embryos from failed eggs of Little Owls *Athene noctua* and Barn Owls *Tyto alba* (outside my study area) show signs of amino acid deficiency, and (4) Tawny Owl chicks grow better on micronutrient-rich one-day old chickens than on mice from the breeding territory, when fed *ad libitum*. The latter was conducted as a pilot study to examine effects of food quality on chick growth in Tawny Owls, as the owls cache food in the nest box, and this food can easily be experimentally replaced. A chick-swap experiment between two nests in 2006 indicated that the variation in nestling growth was related to the location (and parents) where they had been raised and not their place of birth, caused in part by differences in food quality in addition to quantity (unpubl. data). The pilot study experimentally examined whether such differences could have been related to food quality or the variation in food quantity.

METHODS

Owl and raptor surveys

Surveys were conducted for birds of prey and Tawny Owls during 1992–93 and 2006–07 in the southwest part of Veluwe (52°14'N, 5°49'E), a large forested area in central Netherlands. Birds of prey were located by nest searches; from about 15 January until the end of February, playback surveys were used to locate Tawny Owls. In 2003, 12 nest boxes were put up to acquire data on Tawny Owl breeding success. Nest boxes were placed where owls were already present, so the distribution of owls was not altered. Most owls in this area reside in old Beech *Fagus sylvaticus* stands or lanes and breed in cavities (e.g. old nests of Black Woodpecker *Dendroscopus martius*). Tawny Owl nests were checked in mid-March to determine occupation and clutch/brood status. Nest boxes that showed no indication of owl presence in March were revisited in April and May for possible late broods.

Breast muscle condition

During incubation, breeding Tawny Owl females were caught by placing a net in front of the nest box opening (2004, 2006–07). I was able to determine the post egg-laying body condition seven times, in a total of five birds (one bird was caught three times). In Sparrowhawks incubation weight is virtually stable throughout incubation and reflects the weight elevation prior to laying (Newton 1986). This may be a common pattern of weight variation during the breeding season, as similar changes were observed in Blue Tits *Cyanistes caeruleus* (Perrins 1996). During incubation, the Sparrowhawk female retains her breast muscle dystrophy if so incurred during egg formation. In this study, I assumed this to be similar in Tawny Owl females.

Breast muscle condition was determined by folding a copper wire across the bird's sternum, yielding its cross-sectional shape (Bolton *et al.* 1993). This was carefully re-drawn; the actual measurement used was the diameter of the profile, with the base point located 3 mm under the central line of the sternum. Body mass was determined using a 1-kg Pesola scale.

Embryo anomalies in failed eggs
From 1996–2003, failed eggs from nesting Barn Owls and Sparrowhawks were collected throughout The Netherlands by researchers and conservationists. Failed eggs of Little owls were collected in the Achterhoek (P. and W. Beersma, pers. comm.); eggs of Great Tits originated from the southwest part of the Veluwe research area (2001–03). The eggs were analysed for many possible causes of failure in a context much wider than the scope of this paper; here, embryo anomalies that in poultry have been described as a result of amino acid deficiency (Romanoff 1972, Fabri & Kühne 1988) were extracted from the dataset. The occurrence of these anomalies was compared between species and tested using Chi-square analyses. Rare anomalies were left out of the analysis, as the cause of these could have been incidental genetic disorders as equally as nutrient deficiencies.

Replacement feeding and growth measurements
Replacement feeding was started as soon as possible after the chicks had hatched, but the first few days of chick growth were not included in the data analysis. Every evening, just before dark, excess mice were collected from the nest box and replaced by one-day old cockerel chicks. These differ in food quality from mice in having higher levels of carotenoids and riboflavin (vitamin B2), causing more yellowish faeces in owls receiving day-old chicken instead of mice or voles (pers. obs.). The mice that were collected from the nest box were stored frozen. I did this at two nests in 2007, which contained two young owlets. Chick growth was determined daily by body mass (indicative for the consumed amount of food) and beak length. The latter was chosen as it is the only solid part of the chick that can be measured relatively easy using callipers from birth (in the hatchling, the legs are very fleshy and weak, and difficult to measure using callipers). The chicks were made individually recognisable by colouring some of their white down; this was refreshed daily as it wore off in a few days. After eight days of the chicken replacement feeding regime, the owlets were supplementary fed with thawed mice that had previously been collected from the particular nest box, ensuring the continuation of the *ad libitum* feeding regime. Growth measurements continued as before.

RESULTS

From the early 1990s until 2006–07, raptor numbers have greatly declined, whereas the population of Tawny Owls had slightly increased (Table 1). This difference in population development indicates that the causes of population decline in diurnal birds of prey do not apply similarly to owls. This finding is corroborated by the data of breast muscle condition: in recent years there has been a sharp decline in average breast muscle condition of Sparrowhawks, but measurements from owls do not show poor breast muscle condition, except for a single bird that was diseased in the two last years that she was trapped (Fig. 1). The data indicate that amino acid shortages that in Sparrowhawks result in increased nutrient investments from the breast muscle do not occur in Tawny Owls.

Too few failed eggs were collected from Tawny Owls to make a comparison of embryo anomalies with other bird species. However, in Little Owl and Barn Owl embryos, signs of amino acid deficiencies did occur (Table 2). Sparrowhawks showed more amino acid

Table 1. Numbers of territories of raptors and Tawny Owls in the Veluwe forest study area, The Netherlands, before and after the raptor population decline. Unlike diurnal birds of prey, the Tawny Owl population did not crash.

	1992–93	2006–07
Goshawk *Accipiter gentilis*	5	1
Sparrowhawk *Accipiter nisus*	6	2
Buzzard *Buteo buteo*	6	1
Tawny Owl *Strix aluco*	9	12

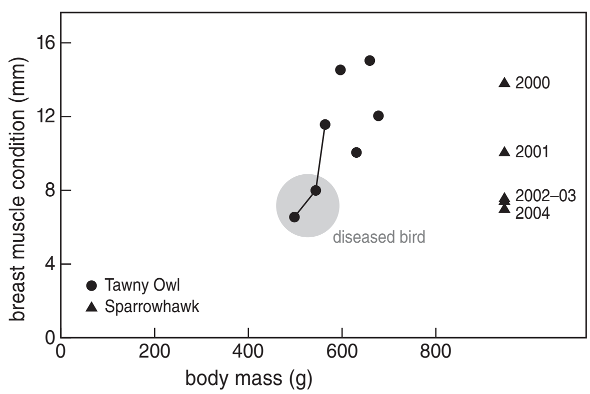

Figure 1. Breast muscle condition after egg-laying in female Tawny Owls (n = 5 individuals) was better than in female Sparrowhawks (indicated are yearly averages). Sample sizes per year in 2000–04 were 10, 6, 14, 14, 14. A single Tawny Owl was caught three times (indicated by drawn line). The second and third time, she had a lame foot and her talons damaged her own foot ('diseased bird'). This bird did produce eggs, but had an overall poor body condition and low body weight.

related embryo deaths in comparison with Little Owls (χ^2_2, $P < 0.025$), but less than Barn Owls (χ^2_2, $P < 0.0001$). In contrast to the results given above, these data suggest that owls (but not necessarily Tawny Owls) do incur reduced reproduction due to amino acid limitation. The occurrence of similar anomalies in Great Tits indicated that amino acid deficiency-related embryo mortality may be widespread in many avian taxa.

Replacement feeding of chicken and mice to Tawny Owl chicks, did not give unambiguous results. In one nest, weight growth was larger during the days the owlets received supplementary chicken, but in the other nest this relation with food type was reversed (Table 3). Beak growth was faster when fed chicken, but only in one chick of each nest. So, results based on beak growth are also inconclusive.

DISCUSSION

This study found very little evidence for a limiting role of poor food quality on reproduction in Tawny Owls. In an area where diurnal birds of prey exhibited signs of amino acid deficiencies, such as poor breast muscle condition after egg-laying and strong population decline, none of this was observed in sympatric Tawny Owls. Rather, observations indicated that Tawny Owls have ways to circumvent amino acid deficiencies in their forest habitat. Perhaps, this is due to a behavioural adaptation, not to produce more eggs than food quality allows. In this way, the breast muscle and population size may be maintained. However, such a strategy would disrupt the more food/more eggs reproductive pattern, unless food quality covaries greatly with food abundance. Given the current ideas of the mechanisms

Table 2. Percentage incidence of embryo anomalies that indicate amino acid deficiency. The occurrence of such anomalies in Great Tits indicated that amino acid deficiency related embryo mortality may be widespread in many avian taxa.

Species	Sparrowhawk *Accipiter nisus*	Little Owl *Athene noctua*	Barn Owl *Tyto alba*	Great Tit *Parus major*
Eggs examined	340	52	204	
Embryos examined	184	24	110	39
Secondary B2 deficiency	35.3	12.5	16.5	
Open brain			5.5	7.7
Lordosis[a]			6.4	
Microphtalmia[b]			12.8	7.7
Coelosomia[c]			6.4	12.8
Extremities backwards			7.3	
Hooked lower jaw			8.3	
Upper beak elongated				12.8
Eye absent				10.3
Total	**35.3**	**12.5**	**63.3**	**51.3**

[a]Lateral S-curvature of the spinal cord.
[b]Underdevelopment of one or both eyes.
[c]Improper formation of the umbilical cord, leaving the internal organs in direct contact with the yolk).

Table 3. Average daily growth rate ±SD of young Tawny Owls, supplementary fed *ad libitum* with chicken or mice from the territory. Indicated is the number of days of a particular feeding regime.

Nest	1		1		2		2	
Chick	1		2		1		2	
	Weight (g)	Beak (mm)	Weight (g)	Beak (mm)	Weight (g)	Beak (mm)	Weight (g)	Beak (mm)
Number of days	6	6	6	6	5	5	5	5
Supplementary food								
Chicken	17.7 ± 5	0.53 ± 0.37	15 ± 6.3	0.32 ± 0.12	21 ± 4.6	0.39 ± 0.19	23.4 ± 9	0.42 ± 0.14
Mice	22.2 ± 8.5	0.33 ± 0.14	21.5 ± 7.2	0.33 ± 0.2	13 ± 7.9	0.36 ± 0.26	17.4 ± 11.5	0.29 ± 0.19

by which food quality in my study area is reduced (long-lasting effects of ongoing nitrogen deposition), the latter correlation is not very likely: the variation in food abundance is expected to substantially exceed variation in food quality. However, this hypothesis cannot be ruled out completely at present and may receive attention in future studies.

Alternatively, owls differ from diurnal raptors by having caeca, blind sacs that are part of the intestinal system (Denbow 2000). In the caeca, birds can recycle uric acid with the aid of bacteria which synthesize amino acids and protein from the uric acid. Birds can absorb the amino acids from the caeca and thus have an additional source of amino acids that diurnal birds of prey do not. For example, if these amino acids are used as fuel, Ptarmigan *Lagopus* spp. were found to acquire 18% of their basal metabolism from recycling their own waste product (Denbow 2000).

If the latter hypothesis is true, replacement feeding experiments to alter amino acid food intake are only feasible for amino acids that cannot be derived from caecal bacteria. If all essential amino acids were produced in the owls' intestine, such an experiment would have no effects. This could explain the results from this study, although, to start with, I cannot be sure that the owlets (and not the adults) actually ate all/most of the one-day old cockerels that were offered. To study the effect of diet on chick growth may require that the owlets be raised in captivity.

The occurrence of embryo anomalies related to amino acid deficiencies seems to contradict all the evidence that amino acid limitation is not very important in owls. However, I expect nutrient-related egg failure to be dependent on reproduction strategy as well as on food quality. Barn Owls invest fewer nutrients per egg than Sparrowhawks (van den Burg 2002), but typically produce larger clutches. Clutch size in Barn Owls appears to be maximized given food availability (r-strategy), whereas in Sparrowhawks (and probably Little Owls) clutch size is optimized (a K-like strategy), given food availability and prey capture rates. So, by minimizing the nutrient input per egg, Barn Owls run the risk of incurring more egg losses due to nutritional shortage, which is largely independent on the amino acid availability in the environment or, more specifically, the Barn Owl food chain. In terms of clutch size and reproductive strategy, Tawny Owls are more similar to Little Owls and Sparrowhawks than to Barn Owls.

As owls have breast muscle mass that they could invest for the benefit of reproduction and potentially contribute to their overall lifetime reproductive success, why do they typically avoid doing so? Perhaps, poor breast muscle condition has significant fitness costs, due to decreased flight performance and, as a result, reduced prey capture rate and increased predation risk. Also, breast muscle decline for the benefit of reproduction may minimize any internal energy store enabling birds to survive starvation (e.g. due to bad weather) or other physiologically stressful conditions (e.g. disease and immune response). In starvation, muscle tissue protein may be especially metabolized to maintain blood sugar levels, as lipid stores cannot serve as source of glucose (Causey Whittow 2000). Species should strive for reproductive success in any given nesting attempt, but should not put themselves at the threshold of survival to do so.

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SAMENVATTING

Enkele gedetailleerde studies bij vogels, onder andere roofvogels, laten zien dat naast de hoeveelheid beschikbaar voedsel ook de kwaliteit hiervan beperkend kan zijn voor de voortplanting en mogelijk de dichtheid van broedparen. Bij uilen wordt de reproductie sterk gestuurd door het prooiaanbod, waardoor effecten van voedselkwaliteit niet worden onderkend. In dit artikel wordt in vier data sets gezocht naar effecten van voedselkwaliteit op de broedbiologie van uilen: (1) populatiegegevens van Bosuilen *Strix aluco* en roofvogels in een verzuurd en door stikstofdepositie aangetast bos op de Veluwe, (2) metingen van de conditie van de vliegspier na de eileg bij Bosuilen en Sperwers *Accipiter nisus*, die in grote mate gebruikmaken van lichaamseiwitten voor de voortplanting, (3) tellingen van aan aminozuurdeficiëntie gerelateerde embryonale afwijkingen bij Kerkuilen *Tyto alba*, Steenuilen *Athene noctua,* Sperwers en Koolmezen *Parus major* (als referentie) en (4) een verkennend onderzoek naar de groei van jonge Bosuilen, waarbij het voedselaanbod experimenteel werd gemanipuleerd (eendagskuikens versus muizen). De populatie Bosuilen was gelijk gebleven in de periode dat de dagroofvogels in dezelfde gebieden sterk in broedaantallen afnamen. Bosuilwijfjes lieten geen grote eiwitinvesteringen van hun borstspieren zien, zoals het geval is bij Sperwers. Embryonale afwijkingen, die bij pluimvee zijn vastgesteld als een gevolg van aminozuurgebrek, werden bij Kerkuilen en Steenuilen gevonden met frequenties van respectievelijk 63% en 12%. Variatie in de groeisnelheid van jonge Bosuilen kon niet worden toegeschreven aan het type voedsel waarmee ze werden bijgevoerd. De beschikbaarheid van aminozuren in de eieren heeft weliswaar een effect op de kwaliteit van de eieren, maar dit is waarschijnlijk meer gerelateerd aan de voortplantingsstrategie dan aan de beschikbaarheid van aminozuren in de voedselketen. Vermoedelijk kunnen uilen essentiële aminozuren winnen uit hun darmblindzakken, waar ze aangemaakt worden door bacteriën. Roofvogels hebben deze blindzakken niet en hierdoor zijn zij waarschijnlijk veel gevoeliger voor aminozuurtekorten in ecosystemen dan uilen.

ARDEA

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