Chapter

Strategies of Owl Reproduction

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Abstract

Sexual reproduction is important to owls because it affords them the opportunity to transfer genes from parents to the offspring. Owls are usually monogamous, and the same mates may pair for breeding purposes for several years, although variations exist from one species to another. Food availability or prey abundance is an important factor that determines reproduction and the upbringing of young ones for owls. Although some species usually engage in breeding during the springs, breeding and raising of chicks usually coincide with the availability of food. Other factors that play significant roles in determining breeding among owls include predation risk, agricultural activities, favourable weather, suitable mate and disease, among others.

Keywords: breeding, gene transfer, fledging, plumage coloration, prey availability, weather

1. Introduction

Breeding period, that is, the period during which nesting and rearing of offspring occurs, is an important period for owls as it is for other animals, because that is the period for gene transfer. It is the period when genes are transferred unto the next generation, from parents to offspring. Breeding takes place during the spring for many species of owls, which has been linked with the availability of prey. The rearing of the offspring is also timed to coincide with the availability of prey.

2. Description and habitat of owls

Owls (*Strigiformes*) have been divided into two families, which are *Tytonidae* and *Strigidae*. *Tytonidae* are the barn owls, while *Strigidae* have near-worldwide distribution [1]. Owls look heavier than they actually are as a result of their dense and soft plumage. Both female and male owls are usually coloured alike. However, males are usually smaller than females of the same species (**Figure 1**).

Owls are nocturnal birds of prey. They feed on prey animals they capture, which may be consumed whole, if the prey animal is not too big to be swallowed, or it may be torn into smaller pieces before being consumed. The indigestible parts of the diet, such as hair, feathers, fur and bones are retrieved from the pellet form through regurgitation after a few hours of consumption.

Figure 1.
Barn owl: lighter colour male (right), female with spottiness (left). Credits: Jason Martin (Source: WEC [2]).

Some of the known and well-studied species of owls are the barn owls (*Tyto alba*), which are sometimes referred to as ghost owls or monkey-faced owls [2], Ural owls (*Strix uralensis*), spotted owls (*Strix occidentalis*) and tawny owls (*Strix aluco*). Barn owls are easily identified by a white or tan underside with black spottiness. The females tend to be darker than the males which are whiter [2]. However, the females

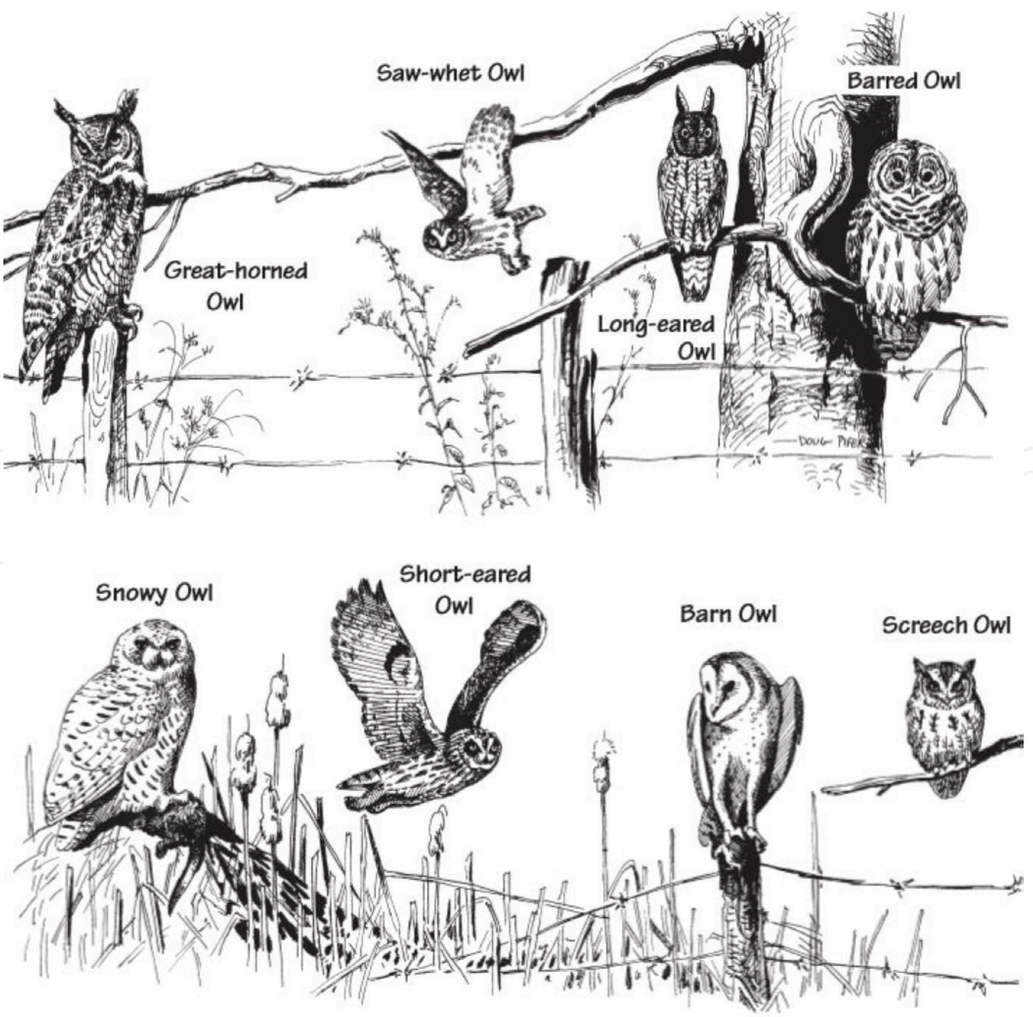

Figure 2.
Species of owls. Credits: Chuck Fergus.

have more speckling than their mates. They also possess relatively small eyes than males, while the males seem to be smaller in body size than the females.

Owls are known to feed mostly on small mammals such as mice, voles, shrews, *Microtus sp.*, *Sigmodon hispidus*, *Rattus rattus*, *Neofiber alleni*, *Sylvilagus palustris*, as well as *Oryzomys palustris* [3–5]. They sometimes also feed on reptiles, amphibians, birds and large insects.

Owls, especially, barn owls find it convenient to inhabit open areas, such as grasslands, agricultural fields and marshes. They may be found nesting in hollow trees or buildings, where human activity is not predominant [2]. Owls do not really make any nests but inhabit abandoned nests of other birds. Being nocturnal birds, they either rest mostly during the daylight or roost in quiet and protected areas. They may be found to defend their immediate nesting areas, but they may not necessarily defend their foraging areas from other owls [8]. Drawings of different species of owls are presented in **Figure 2**.

3. Unique reproductive characteristics of owls

Owls are known to be monogamous. The same mates may stay together for breeding purposes for several years, although variation may exist from one species to another [2, 6–10] The sole responsibility of the female owls during breeding is to lay eggs, incubate and hatch them. It is the responsibility of the male to hunt and provide food for the mate during breeding. The feeding of the mate starts prior to the laying of eggs and continues till about 2 weeks after the eggs are hatched. At about 2 weeks after the eggs are hatched, both parents provide for the brood till they become independent at about 10–12 weeks of age.

4. Factors influencing reproduction among owls

Some of the factors affecting sexual reproduction among owls include:

- food availability;
- weather;
- plumage colouration;
- predation risk;
- age;
- disease;
- mate availability;
- habitat quality;
- agricultural practices;
- placement of nest boxes.

4.1 Food availability

Availability of prey is an important consideration in owl breeding because it affects body condition of the birds. Hence, it could be considered as the most important factor influencing breeding among owls. Availability of prey animals does not only affect body condition of the bird, but it also affects survival of both the parents and the offspring. Availability of food is determined by other factors such as habitat, climate and agricultural activities [3–5, 11–13].

The reproductive success of barn owls was shown to increase with the proportion of voles in the diet, while it was decreased with an increase in the proportion of mice in their diet. Voles seem to have some advantages over mice as a favourite potential prey of owls [4, 14]. Voles are three times the weight of mice [15, 16]. An owl may have to expend three times energy to capture a vole on capturing the equivalent weight of mice. It is logical that it would rather go for a vole than three mice. Availability of voles has been positively correlated with successful reproduction among owls as well as the number of offspring produced [17]. Also, clutch size and juvenile survival have been positively correlated with availability of vole densities [18, 19].

4.2 Weather

During cold temperatures and snow, food or energy requirement for owls increases because of the need for body temperature regulation [7]. The nutrients that could have been channelled for breeding purposes will definitely first be channelled towards survival, unless there is enough to meet both needs. Also, during these cold temperatures, prey may be scarce and difficult to find owing to obstruction. One would have thought that the effect of the cold temperatures would not be so felt by owls because of their plumage, but it has been reported that owl plumage does not provide as much insulation for the body as would have been expected [20]. Also, owls are known to have less fat reserves, through which they would have confronted the harsh weather situation [22]. In a nutshell, harsh weather, especially cold temperature, is an important factor that limits owl breeding through availability of prey and increase in nutrient requirement for owls.

Winter has been reported to be responsible for a great variation in reproduction performance of barn owls [7]. Reproduction was greatly reduced during winter, resulting in major mortality of potential breeders, interference with prey capture and limitation on prey accessibility owing to more energy requirement by the owl for maintenance of its body temperature, required for its survival. In owls, reproductive success is sometimes higher in the more northern latitudes [7]. Reproduction by the northern spotted owl (*Strix occidentalis caurina*) has been shown to be negatively correlated with winter precipitation, while the reproduction by the California spotted owl (*Strix occidentalis occidentalis*) was shown to be positively correlated with rainfall [23,]. Weather and prey availability have been observed as the most important factors influencing breeding among owls [13, 15, 24, 25].

4.3 Plumage colouration

Differences in plumage colouration have been reported to have the tendency to result in behavioural, physiological and fitness variations, among owls [26–28]. Plumage colouration has been linked with improved immune response in owls [29]. It is an important factor that influences the decision of male owls for selection of mates. Research findings have shown that female owls with more spottiness produced chicks with improved immune response, and blood-sucking

flies (*Carnus haemapterus*) were also found to be reduced in nesting associated with females with more spottiness [29, 30]. It is natural for male owls to select females with heavy spottiness, considering factors such as possessing higher reproductive quality.

Female plumage colouration has been positively linked with parasite resistance [29]. It has been suggested that heavily spotted female owls are a prediction of low parasite fecundity. Furthermore, plumage spottiness has been identified as a heritable trait. The male may choose this trait for breeding as an indicator of female genetic quality, being a heritable trait that predicts the offspring's ability to resist parasites [28].

For male owls, lighter coloured male barn owls have been reported to have lower reproductive success than reddish-brown males, as well as not feeding the brood as much as the reddish-brown ones [29]. However, barn owls in the Middle East have been observed to be lighter coloured than those in temperate regions [31]. Darker owls have been reported to have larger wings and tails as well as consume lesser *Muridae* than darker-reddish owls, which were reported to consume more of *Cricetidae* [32].

Research findings have reported an increase in the darker coloured tawny owls in the 2000s, which is suggestive of an adaptation mechanism to global climate warming. Plumage pigmentation has been suggested to be an essential trait of organism's resilience to environmental stress [33, 34]. However, female plumage colouration has not been linked with body size, hatching date, brood size or number of offspring produced [34].

4.4 Predation risk

Another important factor influencing breeding and survival of brood among owls is the occurrence of predation risk. The main predator of owls is diurnal raptor goshawk, *Accipiter gentilis* [35]. Predation by diurnal raptors could account for about 73% of natural tawny owl mortality [36]. A research report revealed that predation was more biased towards breeding females [35]. Breeders and parents may be more exposed to predation because they spend more time out of the nest, hunting to provide for the brood. In years when predation is high, it is logical for breeders to reduce their vulnerability to predation risk by minimizing the quantity of food allocated to the chicks [18]. They may reduce food allocation simply by reducing the breeding rates or by laying smaller clutches. Little wonder then why it has been reported that in years when predation was low, breeding propensity was high [18]. It has been noted that owls with small clutches containing 1–2 eggs, which breed in territories exposed to predation risk, are less likely to complete the breeding attempt compared to those with larger clutches breeding in less exposed territories [37, 38].

In some parts of the world, particularly in the UK, goshawks start to display over territories, nests and building in late March and April. This is at the time when owls in most cases are already committed to breeding; hence, they may be threatened not to complete the breeding attempt if they are exposed [39]. It has been observed that breeding parents as well as those producing more offspring per breeding attempt are often more vulnerable to predation risk than non-breeding parents or those producing fewer offspring. It is a common practice for long-lived parents to reduce their vulnerability in years with high predation risk. They minimize their vulnerability in three essential ways: (a) by abstaining totally from reproductive activities [40]; (b) by reducing the number or quality of offspring produced [41]; or (c) by neglecting the reproductive attempt at an early stage [42].

4.5 Age

Age has been shown to slightly influence sexual preproduction among owls [43]. Breeding propensity increased slightly as female owls aged, although this was only observed for parents who had successfully fledged chicks in the previous year. Female owls who had successfully fledged chicks in the previous year are more likely to reproduce as they age compared to those that had not fledged chicks [18]. Survival and reproduction rates have been observed to be age dependent [44, 45].

4.6 Diseases

Decline in population size and extinction of many wildlife species are resulting from emerging infectious diseases [46], and the spread of these diseases has been noted to be facilitated by the movement of carriers and pathogens arising from environmental alteration owing to change in climate and human activities [47]. The threatened species may be pushed to extinction via decline in breeding performance or as a result of direct mortality [48, 49].

4.7 Mate availability

Since owls undergo sexual reproduction, availability of breeding mates is very important to breeding and its success. In addition to the availability of mate is the issue of closeness to the mate. Familiarity among mates has been observed to improve breeding performance among owls [50]. Breeding dispersal, which is a movement between successive breeding sites [51], has been reported to offer owls the opportunity of avoiding inbreeding among owls, as well as to enhance breeding performance by moving to a better breeding site or pairing with a better mate [52–54]. However, dispersal may result in reduced breeding success as individuals that disperse are not guaranteed of acquiring better territories or mates [55].

4.8 Habitat quality

Owls are sometimes selective when it comes to location for breeding. Barn owls have been reported to prefer to breed in nest boxes that are far away from roads [56]. Breeding in nest boxes close to roads may influence the breeding process as a result of disturbance as well as traffic accidents [4]. Variations in breeding performance of barn owls in the Middle East have been linked to variations in habitat features surrounding the nest boxes [57].

4.9 Agricultural practices

Intensive agricultural practices have been observed as one of the reasons for decline of owls [4], resulting in less grain on the field for small mammals to feed on which consequently reduces the availability of prey animals for owls. The fewer availability of ditches and borders available for rodents to exploit is another factor affecting owls' population [4].

4.10 Placement of nest boxes

It has been observed that having nest boxes in locations where non-arable fields exist may limit the availability of prey animals for owls, as would have been observed in areas with arable crops, which would have enhanced the availability of

prey animals [58]. It has been suggested that barn owls prefer to breed in areas with arable fields due to the availability of a variety of owl diet in the microhabitat [32].

5. Courtship and copulation initiation among owls

Courtship involves calling. The male calls to the female for attention, to attract the female to a suitable nest, although this may vary from one species to another. The calling may be accompanied with the provision of food, by displaying the prey animals.

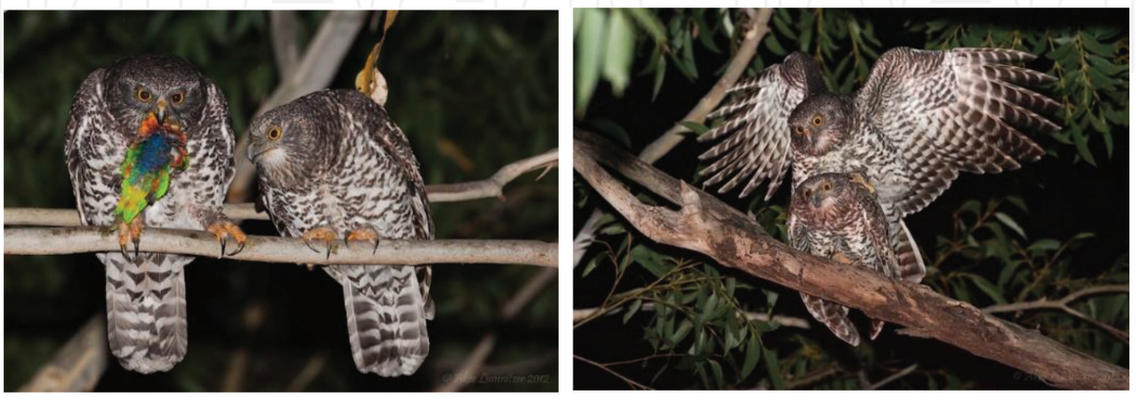

Figure 3.
Owl pair courtship feeding and copulation, female is attracted by food (left); copulation followed acceptance of food (right). Credit Ákos Lumnitzer (Lewis [61]).

Figure 4.
Copulation of owls, the female holding the male's gift in her bill. Source: König, Weick and Becking [10].

Copulation may follow once the female accepts the food (**Figure 3**). In order to initiate breeding among owls, they call and sing. The song plays two important roles, which are for claiming the territory and to attract mates, although the male's song exercise reduces drastically after pairing [9, 10, 59]. Owls looking for mates may sing endlessly until a mate is found. The uniqueness of the female's song over the male's lies in higher pitch and clarity. Males of Tengmalm's owls (*Aegolius funereus*) are known to utter only a few phrases of song whenever they bring food for their mates [9, 10, 59]. Copulation among

owls may take place in rocks, branches or in the nest, with the female carrying the male's gift with which she has been 'bribed' with her bill, as shown in **Figure 4**. Females may wander from nests to nests but males are noted to be more faithful to territories [9, 10]. Owls may inhabit different locations for breeding purposes, Tengmalm's owls, Northern Hawk owls (*Surnia ulula*) and Tawny owls may inhabit tree holes, larger open cavities of tree stumps or natural holes, respectively [9, 10].

6. Laying of eggs

Owls' eggs are white and oval in shape. Laying of eggs may commence in February in temperate environment, while it may begin in June, summer or fall in tropical or subtropical environments. Breeding among owls may commence in late winter in temperate regions and may begin almost at any time in the tropics, especially towards the end of the dry season [9, 10, 59]. The female barn owls usually lay between 4 and 6 eggs, while some species may lay between 1 and 2 eggs, although laying of up to 10 eggs in a single nest has been reported. Eggs are laid at interval of between 2 and 3 days and incubation starts with the first egg laid; hence, the eggs are usually hatched in order in which they are laid. So, the chicks in a single batch are not of the same age (**Figure 5**), an age variation of a few days usually exists among the chicks in a single nest [2]. However, incubation of eggs and hatching among species such as Pygmy owl (*Glaucidium passerinum*) may not commence until the last egg is laid [9, 10].

The implication of the age difference is the nature's unique way of controlling for food availability. In case of food scarcity, it is expected that the older and stronger chicks would survive, and hence, the parents would usually have offspring to continue their generation. However, when food is available, the tendency that all the chicks would survive is high.

Figure 5.
Age difference among barn owl chicks. The one in the middle is the oldest at 14 days old, the one lying down at the extreme left is the youngest at 4 days old, and there is an egg at the centre that is not hatched yet. Credits: Jason Martin (Source: WEC [2]).

7. Incubation, brood size, hatching and growth rate among owls

The average brood size among barn owls has been estimated to be 4.1, while the clutch size is 6. Findings have shown that 6 out of 10 breeding pairs of barn owls

have the capacity to produce two broods per year. The owl average clutch size is 2.85 with about 9.3 out of 10 clutches having 2–4 eggs [18]. Incubation among owls takes about a month. Each chick may reach a fledging stage between 56 and 63 days [2]. A fledging stage is a stage during which a chick learns how to fly. During the fledging stage, provision is still made for the chicks by their parents for another few days, before they eventually become independent to feed themselves.

In general, owls lay between 1 and 13 eggs, depending on the species, although for most species it is 2–5 eggs [60]. Incubation begins with the first egg being laid. During incubation, the eggs are rarely left alone. The female develops a brood patch, which is a sparsely feathered part on the belly, which has higher density of blood vessels than other parts of the skin. The eggs receive warmth directly from the female owl through brood patch. The female owl also develops an egg tooth on the beak, which is required for hatching the eggs [61]. The hatch tooth breaks off after hatching. Fledging age differs from one species of owl to another. It may be somewhere around 4–5 weeks in screech owls, 9–10 weeks in great horned species and 7–8 weeks in barn owls [7, 8, 62, 60]. An owl may become sexually mature at about 1 year of age, although some species may not start breeding until their 2 or 3 year of age. A pair may breed once or twice per year depending on some important factors influencing breeding success [7, 8, 62].

8. Nutritional requirements of breeding owls

When it comes to reproduction and nutrition, animals may be grouped into two in terms of the relative period acquisition and expenditure of nutrients: the income breeders and capital breeders [63]. Income breeders are animals that feed during the

	NBO (n = 5)	BO (n = 5)	U-test	*p*-value
Mass in grams				
Total body mass	311.6 ± 5.0	363.3 ± 5.5	0	0.008
Total body mass feathers	2777.2 ± 6.5	329.1 ± 4.9	0	0.008
Fresh body mass	276.7 ± 6.3	315.0 ± 3.7	0	0.008
Body water	164.8 ± 2.0	209.4 ± 3.7	0	0.008
Dry body mass	111.9 ± 4.4	105.6 ± 3.3	6	ns
Body lipid	41.6 ± 3.3	26.2 ± 3..2	2	0.032
Body protein	55.4 ± 0.8	61.6 ± 0.6	0	0.008
Body mineral	14.9 ± 0.4	17.8 ± 0.8	0	0.008
Water/protein	3.0 ± 0.1	3.4 ± 0.1	0	0.008
Fresh mass content in percentage of fresh body mass				
Water	59.7 ± 0.7	66.5 ± 1.0	0	0.008
Lipid	14.9 ± 0.9	8.3 ± 1.0	0	0.008
Protein	20.0 ± 0.2	19.6 ± 0.2	4	ns
Mineral	5.4 ± 0.1	5.6 ± 0.2	12	ns
Dry mass content in percentage of dry body mass				
Lipid	36.8 ±1.5	24.5 ± 2.3	0	0.008
Protein	49.8 ± 1.3	58.6 ± 2.0	0	0.008
Mineral	13.4 ± 0.4	16.9 ± 0.6		0.016

ns = non-significant.
Source: Durant et al. [67].

Table 1.
Body composition of breeding (BO) and non-breeding barn owls (NBO).

	Yolk	Albumen and shell	Total
Mass in grams			
Fresh mass	17.60 ± 0.20	4.30 ± 0.10	13.3 ± 0.30
Dry mass	4.10 ± 0.06	1.54 ± 0.02	2.56 ± 0.06
Protein	1.62 ± 0.03	0.49 ± 0.01	1.13 ± 0.03
Lipid	1.00 ± 0.02	1.00 ± 0.02	0.00 ± 0.00
Mineral	1.48 ± 0.04	0.05 ± 0.01	1.43 ± 0.04
Energy in kJ			
Protein	27.1 ± 0.50	8.30 ± 0.20	18.80 ± 0.50
Lipid	37.8 ± 0.60	37.5 ± 0.60	0.30 ± 0.10
Total	64.90 ± 0.80	45.8 ± 0.70	19.10 ± 0.50
Energy content in kJ g^{-1}			
Dry mass	15.80 ± 0.20	29.80 ± 0.10	7.50 ± 0.10
Fresh mass	3.70 ± 0.10	10.80 ± 0.20	1.40 ± 0.10

Source: *Durant et al. [67].*

Table 2.
Composition and energy content of barn owl eggs.

reproductive cycle in order to cover their reproductive expenditure. On the other hand, capital breeders are those animals that build their body reserves before the commencement of the breeding cycle. Such animals cover their reproductive expenditure from the stored-up food, eaten before the reproduction starts. Owls are income breeders, they feed during breeding to cover their reproductive expenditure [64, 65].

No difference has been observed in the body mass of barn owl during the laying period, which may imply that not all the nutrients stored during pre-laying were used for egg formation. **Tables 1** and **2** show the body content of breeding and non-breeding owls and egg contents of owls, respectively. In essence, it can be said that all the essential nutrients required by female owls for egg formation can be obtained by routine feeding during breeding [66–68], although it is important for minerals to temporarily accumulate in the bone before the commencement of laying.

Female owls may not require long periods of nutritional preparation before reproductive attempt is initiated [66]. In fact, a second clutch may be laid about 2 weeks after the first clutch. A starved female owl was found to return to laying about 28 days after being subjected to prolonged total food deprivation, up to a relative body mass loss of 30% [69]. This finding supports the claim that breeding is not influenced by stored energy or nutrients, neither is it initiated by reaching an optimum body condition. It may also imply that climatic and poor body condition of female owls do not have a long-term effect on breeding.

9. Conclusion

Owls are often monogamous with slight variations among species. They are income breeders, hence do not require special feeding plan prior to breeding or during breeding. The nutrient requirement for body condition and egg formation are usually met through routine feeding. Food availability, predation risk, weather and availability of sexual mates play important roles in determining sexual reproduction among owls. A difference of 2 or 3 days exists between the laying of one egg and

the other. The eggs are hatched in the order in which they are laid, after incubation cycle is complete, which usually takes about 33 days.

Acknowledgements

I appreciate the privilege to re-use the photos and drawings by Jason Martin and Chuck Fergus, respectively.

Conflict of interest

I have no conflict of interest regarding this contribution.

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