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Owls

Edited by Heimo Mikkola



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Published in London, United Kingdom



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<http://dx.doi.org/10.5772/intechopen.80242>

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First published in London, United Kingdom, 2020 by IntechOpen

IntechOpen is the global imprint of INTECHOPEN LIMITED, registered in England and Wales, registration number: 11086078, 7th floor, 10 Lower Thames Street, London, EC3R 6AF, United Kingdom

Printed in Croatia

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library

Additional hard and PDF copies can be obtained from orders@intechopen.com

Owls

Edited by Heimo Mikkola

p. cm.

Print ISBN 978-1-78984-053-7

Online ISBN 978-1-78984-054-4

eBook (PDF) ISBN 978-1-83880-461-9

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Meet the editor



Heimo Mikkola received his PhD degree in Applied Zoology and Limnology from the University of Kuopio, Finland and his thesis was on Ecological Relationships in European owls.

Partly based on that academic work, he wrote a very popular book “Owls of Europe” published in 1983 in the UK. Since 1988, he has been an adjunct Professor of the Eastern Finland University but instead of Finland he has worked mainly abroad for well over 30 years in Africa (22 years), South America (6 years) and Central and South-east Asia (4 years) mainly with the African Development Bank and the United Nations. During these years, he has had many opportunities to visit and study owls in over 130 countries. In many of the countries he undertook public interviews to gain insight in to how people see the owls and their conservation. Some rarely known owl beliefs in Central Asia are included in this book. Owl studies often took him to the best bat biotopes as well, and he started to collect data on bats eaten by owls. In 2014, he was given the title of “Champion of Owls” in Houston, USA, mainly because of his six worldwide distributed and translated owl books. Thus far he has written 220 papers and books on owls, and recently a Japanese edition of his “Owls of the World” book was published in Tokyo.

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Preface

Owls have held a special fascination for humans for thousands of years. And owls are one of the world's oldest species of Vertebrate. Fossil remains dating back 60 million years have been found and these reveal that owls have changed very little in that time [1]. Practically every culture has a story to tell about owls. Considering all these stories together, they form a perplexing composite.

It is a paradox that owls are one of the most beneficial group of birds, but also one of the least understood [2]. Few other birds or animals have gathered so many different and contradictory beliefs about them: owls have been both feared and venerated, despised and admired, considered wise and foolish, associated with witchcraft, medicine, weather, births and deaths – and have even found their way into *haute cuisine* [3].

Folklore has it that owls are birds of ill omen and that deception is one of their favourite ploys. Contrary to this, it must be said that the owl has been widely admired through the ages by deities, scholars, poets and animal lovers in general [4]. Owls have also appeared on artefacts such as Peruvian Moche pottery jugs, North American Indian pipes and shields, on African masks, and delicate Chinese and Japanese paintings [5].

With their unearthly nocturnal calls, their humanlike faces and piercing binocular vision, members of the owl family *Strigidae* have provoked a deep and universal response in human beings.



Large, piercing all-seeing eyes. Photo: Courtesy of Johan J. Ingles.

One purpose of this book is to point the way towards a better understanding on how owls relate to their environment and how important it is for us to use that environment more wisely. But conservation success for living creatures, including owls, depends not only on environmental issues, but also on social and cultural matters. The value of people's participation in resolving complex conservation issues has been rediscovered only lately [6, 7].

I wish to acknowledge the enthusiastic and helpful attitude of the Author Service Manager Lada Božić - without her efforts this book would never have been published.

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Introductory Chapter: Why the Number of Owl Species in the World Continues Increasing?

Heimo Mikkola

1. Introduction

Owls comprise a distinct and easily recognized group of birds. However, similarities in plumage and morphology, coupled with general lack of knowledge of the ecology and behaviour of many species, have led to considerable uncertainty regarding species and even generic limits. The internal taxonomy of owls (*Strigiformes*) may be in a greater state of flux than in any other family of non-passerine birds. The meaning of the term ‘species’ has gone through many changes, driven onwards by new methods, the differing priorities of each scientific age and the varied field of biological research. Four basic species definitions will be given but there are nowadays at least 26 different definitions. Owls have the lowest hybridization rate amongst studied bird groups being only about 1%, whilst game birds are hybridizing over 20% and the swan, geese, and duck group over 40%. Therefore, the biological species concept (BSC) serves still quite well with owls. However, all species definitions have been shown to have their limitations. The BSC shows that species are the real and fundamental units of evolution. The main problem with the morphological species concept is the question of how different two groups must be before they can be called separate species. Evolutionary species concept is very appealing but discovering the precise evolutionary history of organisms is practically impossible. Many owls are so rare that it has not been possible to get blood samples to examine nucleotide sequences in the cytochrome-b gene. Molecular data exists this far only for some 175 species, so 100 or more species waits for official confirmation when new material for DNA-testing becomes available. The discovery of the DNA code revolutionized taxonomy, but the problem is that variability in DNA is often not correlated to variability in morphology or reproductive compatibility. It is obviously unrealistic to assume that we can impose and apply any single definition on a natural world made restless by evolutionary change.

The number of world owl species has gone up from 109 to 268 between 1972 and 2014. This chapter seeks to answer the question: “Why we are getting so many new owl species every year?” One of the main reasons for this is that many owls live on small islands where they develop slight differences from their close relatives on the nearby mainland. It then becomes a matter of taste as to whether you consider one of these isolated populations of owls as a distinct species or not. If you are an objective zoologist you will likely lump the two together as subspecies, but if instead you are a passionate conservationist you will view the island form as a very rare and full species that needs urgent protection.

To significant extent these ‘new owls’ have been known to the scientific community as subspecies correctly (or erroneously!) declared as such. To a much smaller

degree there are still completely unknown owl species being identified in the tropical forests. However, only some 15 totally new owl species have been described after 2001. Details will be given on most recent of these new species. What is sure that we may lose some of the rarest owls very easily if not taking care of the habitat destruction and climate change. If describing them as new species rather than new subspecies helps our conservation efforts—so be it. With the present rate of habitat loss and climate change we will soon lose species faster than to describe the new ones.

Although owls comprise a distinct and easily recognized group of birds, similarities in plumage and morphology, coupled with general lack of knowledge of the ecology and behaviour of many species, have led to considerable uncertainty regarding species and even generic limits. The internal taxonomy of owls may be in a greater state of turmoil than in any other family of non-passerine birds.

2. What are ‘species’

The meaning of the term ‘species’ has gone through many changes, driven onwards by new methods, the differing priorities of each scientific age and the varied field of biological research. The issue of species delimitation has long been confused with that of species conceptualization, leading to a half century of controversy concerning both the definition of the species category and methods for inferring the boundaries and numbers of species. The biggest problem is that currently many biologists advocate different and at least partially incompatible species concepts [1]. Mayden [2] listed 22 named species concepts, and now there are even more alternative definitions (see Appendix 1). This is encouraging biologists to develop new methods of species delimitation that are not tied to traditional species concept; species criteria; species delimitation. Therefore, I will present here only four basic species definitions:

- Biological species concept—a group of actually or potentially interbreeding populations, which are reproductively, isolated from other such groups
- Morphological species definition—a species is defined by a given set of common morphological features not shared by other groups
- Evolutionary species concept—a species is defined by its shared evolutionary history and descent from a common ancestor
- Genotypic cluster definition—a recently introduced definition, which is essentially a genetic version of the morphological definition. Genetic rather than morphological gaps identify the distinctions between species.

3. Problems with these definitions

Owls have the lowest hybridization rate amongst studied bird groups being only about 1%, whilst game birds are hybridizing over 20% and the swan, geese, and duck group over 40% [3]. Therefore, the biological species concept (BSC) serves still quite well with owls. However, all species definitions have been shown to have their limitations. The BSC encapsulates the idea that species are the real and fundamental units of evolution, while higher taxonomic categories such as genera, families and orders are more artificial collection made for convenience, though loosely reflecting

evolutionary relationships. Several authors have called attention to the situations in which adoption of the BSC leads to the recognition of fewer species taxa than adoption of one of the alternative species concepts, such as the diagnosable version of the phylogenetic species concept (e.g. [4, 5]). The main problem with the morphological species concept is the question of how different two groups have to be before they can be called separate species. Evolutionary species concept is very appealing but discovering the precise evolutionary history of organisms is practically impossible. The discovery of the DNA code revolutionized taxonomy, but the problem is that variability in DNA is often not correlated to variability in morphology or reproductive compatibility. It is obviously unrealistic to assume that we can impose and apply any single definition on a natural world made restless by evolutionary change. All the species concepts seem to have some merits and they are all based on important biological properties [6]. Unfortunately, distinct species concepts, despite sharing a common fundamental element, can often lead to different conclusions concerning which population lineages deserve to be recognized as species.

4. First ‘Owls of the World’

In 1972 I was invited to participate in writing the first ‘Owls of the World’ edited by John A Burton [7]. That was a team of 15 people and we attempted to write about and to illustrate every known species of owl. That time it was quite easy to agree that there some 130–140 species of owls, although same year two East German scientists came with a revolutionary reduction of owl species to 109 [8, 9]. They united for instance Barred Owl (*Strix varia*) and Ural Owl (*Strix uralensis*) and had only nine Tytonidae owls (when the number nowadays is 26 or 27 as in **Table 1**). They also correctly united *Bubo* and *Ketupa* but not *Bubo* and *Nyctea*, and included *Ciccaba* to *Strix* and *Rhinoptynx* to *Asio*, etc.

5. Handbook of the birds of the world

In the Handbook [10] I was asked to compile a list for the owls, and ended up in having 205 species in 1999, but König et al. [11] lifted same year the number of species to 212 (**Table 1**). To question this ‘fabrication’ of new species I wrote already in 2000 on the subject “Owl Taxonomy—Where have all the “lumpers” gone [12].

Author	1	2	3	4	5	6	7	8	9
Tytonidae	11	10	16	11	26	16	16	26	27
Strigidae	133	120	189	201	224	183	192	223	241
Total	144	130	205	212	250	198	208	249	268

1 = 1940 [17], 2 = 1973 [7], 3 = 1999 [18], 4 = 1999 [11], 5 = 2008 [15], 6 = 2009 [14], 7 = 2011 [19], 8 = 2012 [20] and 9 = 2013 [21].

Table 1.
 Number of owl species in the world from 1940 to 2013.

6. Taxonomists

Taxonomy is a scientific discipline that has provided the universal naming and classification system of biodiversity for centuries and continues effectively

to accommodate new knowledge [13]. However, there is a saying that if there are two taxonomists in one room, they cannot agree on anything. So, no wonder that owl taxonomy is still in a state of flux and the number of acceptable species varies between 200 and 270. In his book ‘Owl’ renowned Oxford based Dr. of Zoology, Desmond Morris [14] gave a new classification which accepted 198 kinds of owls as genuine species. But the latest ‘Owls of the World’ König et al. [15] listed already 250 owl species and 29 subspecies which could be considered as new and valid species. Personally, I found Morris’ list more appealing [16].

7. First ‘Owls of the World—A Photographic Guide’

But then 2010 I was asked to write *Owls of the World—A Photographic Guide* [20] with the instructions from my publisher to write about and to illustrate every known species of owls of the world. So, after König’s [15] 250 species I ended up in having 249 by expecting that the New Zealand Laughing Owl *Sceloglaux albifacies* is extinct as there are no records since the 1930s.

8. Second ‘Owls of the World—A Photographic Guide’

More than 15 new owl species were proposed immediately after the first edition was printed in 2012. As the book missed so many new species the publisher decided that there was a need to produce a second edition which I did next year with 268 species [21].

9. Future ‘Owls of the World—A Photographic Guide’

After writing the second edition at least five certainly new species have been described as Walden’s Scops Owl *Otus modestus* from the Andaman Islands in the Indian Ocean [22] and Rinjani Scops Owl *Otus jolandae* from Lombok island, Indonesia [23]. Interestingly a thought to be new species as Omani Owl *Strix omanensis* from Oman [24] has now been reidentified as Hume’s Owl *Strix butleri* first described by A. Hume in 1878 [25] based on a single specimen from Pakistan.



Figure 1. Desert Tawny Owl *Strix hadorami* in Israel. Photo: Courtesy of Amir Ben Dov.

The other, more familiar species (**Figure 1**), earlier believed to be *Strix butleri*, from Middle East has accordingly been renamed as the Desert Owl or Desert Tawny Owl *S. hadorami* [26].

Even Europe got recently a new owl species, when the taxonomy of Cyprus Scops Owl *Otus cyprius* (**Figure 2**) was reprised in 2015 [27]. And Maghreb (Coastal plains from Morocco to Libya) got its own Tawny Owl as Maghreb Wood Owl *Strix mauritanica* first proposed by Robb et al. [24] and confirmed by Isenmann and Thévenot [28].

Finally, we have now a long waited official confirmation for a new *Megascops* from the Sierra Nevada de Santa Marta (**Figure 3**), Colombia as *Megascops gilesi* [29]. In South America there are still likely to be some new owl species in Brazil, Colombia, Costa Rica, Ecuador, Panama, Peru and Venezuela. It is very promising that the Neotropical Ornithologists are very active and productive so very soon we will hear more about these new owl species in South America [30, 31].



Figure 2. Latest new owl species in Europe: Cyprus Scops Owl *Otus cyprius*. Photo: Courtesy of Tasso Leventis.



Figure 3. Santa Marta Screech Owl *Megascops gilesi*, Colombia. Photo: Courtesy of Jon Hornbuckle.

10. Why so many new owls?

One might ask where all the newly discovered owl species come from. Is it because of the new genetic research?

Many owls are so rare that it has not been possible to get blood samples to examine nucleotide sequences in the cytochrome-b gene. Molecular data exists this far only for some 175 species, so 100 or more species waits for official confirmation when new material for DNA-testing becomes available.

To significant extent these ‘new owls’ have been known to the scientific community as subspecies erroneously (or correctly?) declared as such. To a much smaller degree there are still completely unknown owl species being identified in the tropical forests. However, only 15 ‘new’ owl species have been described after 2001 as shown below:

Number of owls described:

1800	23
1900	173
2000	62
2013	10
2019	5

Desmond Morris [14] has presented a very good reasoning why we are getting so many new owl species every year: “Today authorities vary considerably in their opinions concerning exactly how many species of owls there are. Some accept as few as 150, while others list as many as 220 (and as stated above—the latest ‘Owls of the World’ even 268—Authors’ comment). One of the main reasons for this huge discrepancy is that many owls live on small islands where they develop slight differences from their close relatives on the nearby mainland. It then becomes a matter of taste as to whether you consider one of these isolated populations of owls as a distinct species

or not. For example, there is kind of barn owl that is found on the Andaman Islands in the Indian Ocean. It is significantly smaller than the mainland form, but because the two never encounter one another in the wild it is impossible to tell whether, if they did meet, they would freely interbreed or remain separate. So, one can only guess as to whether they are genuinely distinct species or not. If you happen to be an objective zoologist you are likely to lump the two together as races of the same species, but if instead you are a passionate conservationist you are more likely to view the island form as a distinct and therefore very rare species that needs urgent protection.

11. So how many owl species we have?

It seems to be impossible to answer that question with our present knowledge and it may take some time to find a balance between the two extremes as they are so far apart; i.e., 198 vs. 268. Personally, I find Morris' number [14] more appealing than my own [21] but due to 'political pressure' I am likely to write third edition of 'Owls of the World' with some 275 species! What is sure that we may lose some of the rarest owls very easily if not taking care of the habitat destruction and climate change. If describing them as new species rather than new subspecies helps our conservation efforts—so be it. With the present rate of habitat loss and climate change we will soon lose species faster than we are able to describe the new ones.

A. Appendix 1. A list of 26 species “Concepts” [32]

1. Agamospecies

Synonyms: Microspecies, paraspecies, pseudospecies, semispecies, quasispecies, and genomospecies

2. Autapomorphic species (see Phylopecies)

3. Biospecies

Synonyms: Syngen, speciationist species concept

Related concepts: Biological species concept, genetic species, and isolation species

4. Cladospecies

Synonyms: Internodal species concept, Hennigian species concept, Hennigian convention

5. Cohesion species

Synonyms: Cohesive individual (in part)

6. Compilospecies

Synonyms: None

Related concepts: Introgressive taxa

7. Composite species

Synonyms: Phylopecies (in part), internodal species (in part) and cladospecies (in part)

8. Ecospecies

Synonyms: Ecotypes

Related concepts: Evolutionary species

9. Evolutionary species

Synonyms: Unit of evolution, evolutionary group

Related concepts: Evolutionary significant unit

10. Evolutionary significant unit

Synonyms: Biospecies (in part) and evolutionary species (in part)

11. Genealogical concordance species

Synonyms: Biospecies (in part), cladospecies (in part), and phylopecies (in part)

12. Genic species

Synonyms: None

Related concepts: Genealogical concordance species, genetic species (in part), biospecies (in part), and autapomorphic species (in part)

13. Genetic species

Synonyms: Gentes (sing. Gents)

Related concepts: Biospecies, phenospecies, morphospecies and genomospecies

14. Genotypic cluster

Synonyms: Polythetic species

Related concepts: Agamospecies, biospecies, genetic species, Hennigian species, morphospecies, non-dimensional species, phenospecies, autapomorphic phylopecies, successional species, taxonomic species, and genomospecies

15. Hennigian species

Synonyms: Biospecies (in part), cladospecies (in part), phylopecies (in part), and internodal species

16. Internodal species

Synonyms: Cladospecies and Hennigian species (in part), and phylopecies

17. Least inclusive taxonomic unit (LITUs)

Synonyms: Evolutionary group (in part), and phylopecies

18. Morphospecies

Synonyms: Classical species, Linnaean species

Related concepts: Linnean species, binoms, phenospecies, monothetic species, monotypes, and taxonomic species

19. Non-dimensional species

Synonyms: Folk taxonomical kinds

Related concepts: Biospecies, genetic species, morphospecies, paleospecies, successional species, and taxonomic species

20. Nothospecies

Synonyms: Hybrid species, and reticulate species

Related concepts: Compilospecies, horizontal or lateral genetic transfer

21. Phylopecies and phylogenetic taxon species

Synonyms: Autapomorphic phylopecies, monophyletic phylopecies, minimal monophyletic units, monophyletic species, lineages

Related concepts: Similar to internodal species, cladospecies, composite species, and least inclusive taxonomic units

22. Phenospecies

Synonyms: Phena (sing. Phenon), operational taxonomic unit

Related concepts: Biospecies, genetic concordance species, morphospecies, non-dimensional species, phylopecies (in part), phenospecies, successional species, taxonomic species, quasispecies, viral species, and genomospecies (bacterial)

23. Recognition species

Synonyms: Specific mate recognition system

Related concepts: Biospecies

24. Reproductive competition species

Synonyms: Hypermodern species concept, and biospecies (in part)

25. Successional species

Synonyms: Paleospecies, evolutionary species (in part), and chronospecies

26. Taxonomic species

Synonyms: Cynical species concept


Related concepts: Agamospecies, genealogical concordance species, morphospecies, phenospecies, and phylopecies

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Strategies of Owl Reproduction

Isaac Oluseun Adejumo

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

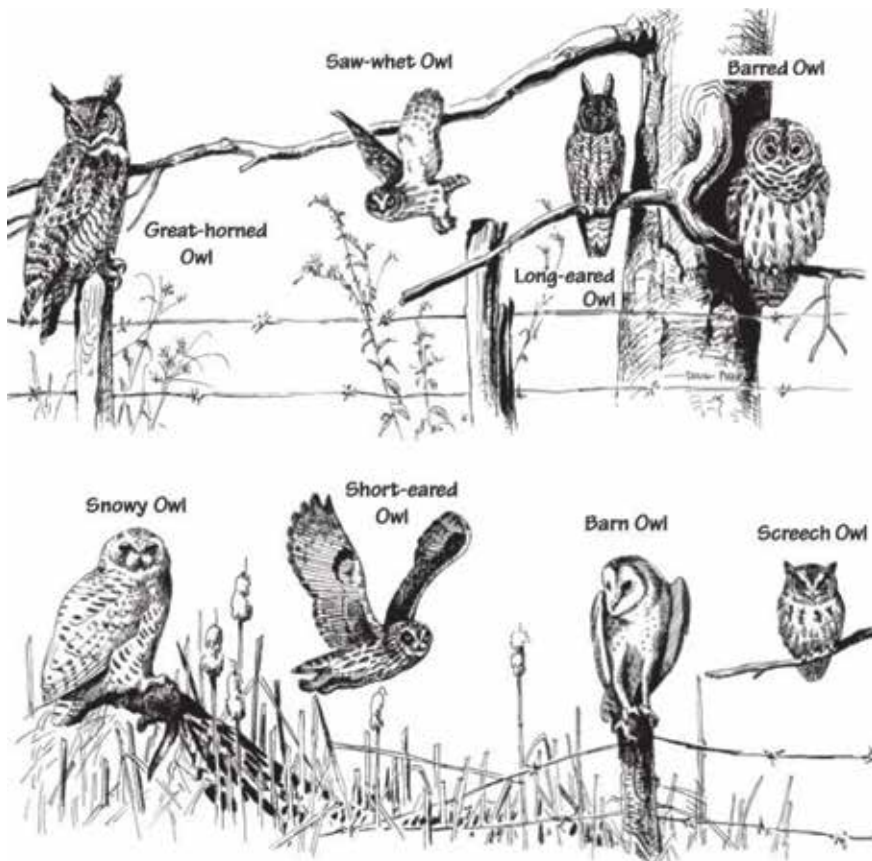


Figure 2.
Species of owls. Credits: Chuck Fergus.

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 Lummitzer (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	271 ± 0.50	8.30 ± 0.20	18.80 ± 0.50
Lipid	378 ± 0.60	375 ± 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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Bird Behaviour during Prey-Predator Interaction in a Tropical Forest in México

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Abstract

Birds emit alarm calls, considered as honest signals, because they communicate the presence of a predator or potential threat. We evaluated behavioural events of birds responding to vocal and visual stimuli of a nocturnal predator (black-and-white owl *Ciccaba nigrolineata*) and a diurnal predator (collared forest falcon *Micrastur semitorquatus*). We analysed variations in behavioural events seasonally (reproductive and nonbreeding) and by bird size, as well as their relationship with the vegetation structure and landscape. The study was performed during the breeding (March-May) and non-breeding seasons (February, June and July) of 2016 in Chiapas, Mexico. We used four transects with different vegetation types and land uses. The most frequent behavioural response by birds to the vocal stimuli of the black-and-white owl and the collared forest-falcons was vocal, during the breeding season, and small species responded the most to the stimuli ($p = 0.008$) and ($p < 0.015$), respectively. We identified two vegetation and two landscape variables associated in 36% of probability for the prey to respond to black-and-white owl vocal stimuli, three variables of vegetation and one of the landscape in 37% for the collared forest-falcon stimuli. Potential prey animals modify the behaviour, which allows them to detect, evade or confront a predator.

Keywords: signs, *Ciccaba nigrolineata*, *Micrastur semitorquatus*, stimuli, mobbing, environmental variables

1. Introduction

Ecological interactions are the basic components that structure and stabilise the biological diversity of ecosystems and are important for communication among individuals [1, 2]. Communication involves the transmission of information (signals) from one individual to another [3]. Signals are the exchange of information from a sender (individuals) that provokes the response of a receiver; they may be conspecific or hetero-specific [3–5]. There are three types of signals between individuals: visual, vocal and olfactory. In the case of prey-predator interaction, visual recognition of a predator relies on previous experience, while vocal recognition involves learning to detect the presence of predators [5, 6].

Birds make alarm calls that are honest signals (i.e. it implies a benefit to the sender and/or receiver), and these signals are used to alert the presence of a potential predator or threat [3, 7, 8]. Predators limit the abundance of their prey populations [9, 10]. However, prey availability may be a factor regulating the abundance of predators [11]. Mobbing (i.e. aggregations or harassment [12, 13]) is considered a behaviour in birds to deal with predators; it is carried out by bird species at a risk of predation or other potential threats, which are identified visually or vocally [14, 15]. Mobbing is considered an anti-predator adaptation for survival and reproduction [16, 17]. In some bird species, the intensity of mobbing varies temporarily. For example, the mobbing behaviour of the European pied flycatcher (*Ficedula hypoleuca*), the American robin (*Turdus migratorius*) and the house finch (*Haemorhous mexicanus*) is more intense during the breeding season because they defend their territory and share parental care [13, 18–20]. Also, the costs and benefits of being a participant in mobbing vary according to the size of the bird. Small species can unite to avoid being attacked since they are often more easily depredated alone [15, 21]. On the contrary, birds of greater size are more difficult to depredate [15, 22].

Response behaviours (e.g. attacking, fleeing and vocalising) of prey are influenced by environmental factors and previous experience of the organism [23]. Most species exhibit aggressive-defensive behaviours such as threatening gestures, body postures (different body positions of head or wings) and attacks or may show submission behaviours such as escaping or standing still [23]. One way to evaluate the different response behaviours of birds is through the playing of pre-recorded vocalisations and by providing visual stimuli of their potential predators [24]. The use of vocal and visual stimuli of the predators allows for evaluating the response behaviour of the potential prey [13, 24].

Prey responds to the risk of depredation by altering its behaviour (e.g. changes in vigilance or in the search for food) or by avoiding high-risk areas [25]. These changes in behaviour allow prey to escape approximately 80% of the time from attempts to be caught by predators [26]. Therefore, prey can learn and thereby respond to distinct levels of risk and fear of predation [27, 28]. According to the ‘ecology of fear’ theory, the prey will avoid areas of predator abundance to reduce the probability of being depredated or will use suitable sites to rapidly escape [28]. It is important to study the prey-predator relationships to completely understand such interactions. In this context, the objectives of this study were to analyse the bird behaviours that respond to vocal and visual stimuli of a nocturnal raptor, the black-and-white owl, and a diurnal, the collared forest falcon between seasons, bird sizes and their relation to the vegetation structure and landscape.

2. Materials and methods

2.1 Study area

The study was carried out in the La Selva El Ocote Biosphere Reserve (REBISO), located in the northwestern portion of the state of Chiapas (between 16° 45' 42" and 17° 09' 00" North; 93° 54' 19" and 93° 21' 20" West; **Figure 1**). The reserve covers an area of 101,288 ha, with elevations ranging from 200 to 1450 m a.s.l. [29]. Emilio Rabasa Ejido is located in the buffer zone and characterised by a semi-deciduous forest landscape, secondary vegetation and different land uses such as pasture, agricultural fields and human settlements [29]. The sampling points covered diverse types of vegetation and land use.

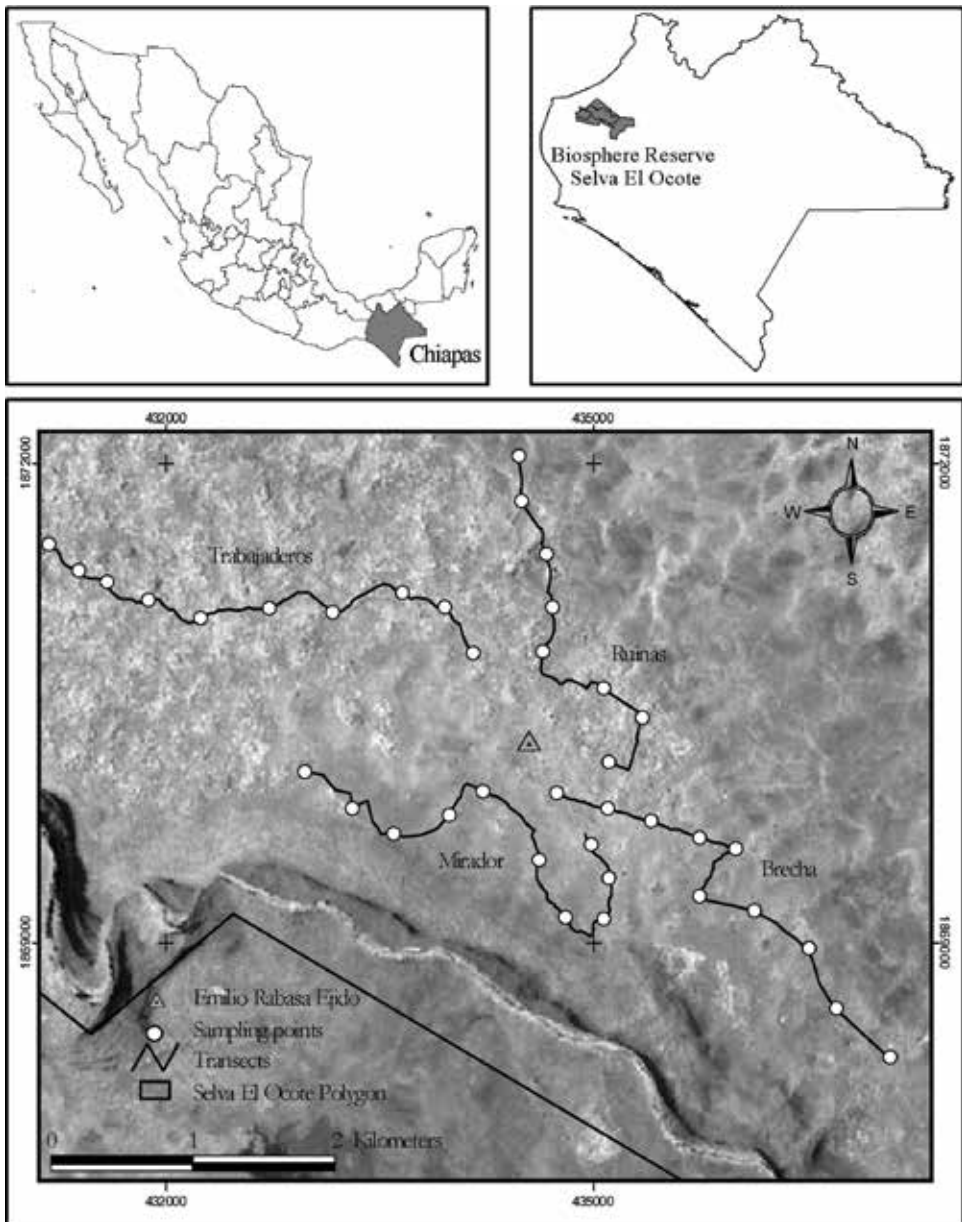


Figure 1.
Geographic location of four transects and sampled points in La Selva El Ocote Biosphere Reserve, Chiapas, Mexico.

2.2 Predatory species used as a model

Nine nocturnal species of raptors have been recorded in the La Selva El Ocote Biosphere Reserve [30]. Three of them (black-and-white owl, *Ciccaba nigrolineata*; ferruginous pygmy owl, *Glaucidium brasilianum*; and spectacled owl, *Pulsatrix perspicillata*) include birds in their diet [31–33]. Twenty-five diurnal raptors have also been recorded [30], of which the collared forest falcon and the barred forest falcon (*M. ruficollis*) feed mainly on birds [33, 34]. The predators used as a model in this study were selected based on their dietary habits (mainly birds) and hunting

behaviour in the interior of the forest [34]. We selected the black-and-white owl and the collared forest falcon as the best that met these criteria.

2.3 Description of the predators

The black-and-white owl is a medium-sized owl (average 39 cm) with a wide distribution in the Neotropical region and apparently stable populations [35]. However, its populations may be locally declining because of habitat transformation or fragmentation. This species feeds on small birds such as thrushes (*Turdus* sp.), burnished-buff tanager (*Tangara cayana*), blue-grey tanager (*Thraupis episcopus*) and silver-beaked tanager (*Ramphocelus carbo*) [31, 36].

The collared forest falcon is a medium-size forest hawk (average 55 cm) which feeds on birds and small mammals [34]. Species of birds reported as its prey include the crested guan (*Penelope purpurascens*), the great curassow (*Crax rubra*), the plain chachalaca (*Ortalis vetula*), the spotted wood quail (*Odontophorus guttatus*), the keel-billed toucan (*Ramphastos sulfuratus*), the golden-fronted woodpecker (*Melanerpes aurifrons*) and the brown jay (*Cyanocorax morio*) [34, 37].

2.4 Field methods

In previous surveys during February and August 2015, the *ad libitum* recording method was used, which consists of opportunistic observations of behavioural events, without restrictions on time and observations (of bird species), on a continuous basis [38, 39]. With this method, behavioural events (short-term behavioural patterns that can be expressed as frequencies [38]) of some birds were recorded during the emission of vocal stimuli of the black-and-white owl and the collared forest falcon calls. Based on these observations and with references from the literature [22, 40, 41], we obtained an ethogram of the description of species' behaviour [38] (Table 1). With this ethogram, the birds' behaviour was classified into nine categories, which were used as a basis for determining the behaviour

Behavior category	Behavior	Detection type	Description
Silent answer	still	Visual	Individual is without any movement, standing or in rest position
Silent response with movement	vigilance, without vocalizing	Visual	It moves from one place to another, using the legs (soil, branches) and observes its surroundings turning head and body
Silent response with movement	escape	Visual	Individual moves away from the site and does not return
Response with movement	escape - vocalizing	Visual, vocal	Individual moves away from the site vocalizing
Low intensity mobbing	vigilance-vocalizing	Visual, vocal	It moves from one place to another, using the legs (soil, branches)vocalizing
Low intensity mobbing	vocalize (alarm call)	Vocal	Vocalization can be loud and repetitive or sporadic and performed when there is a danger signal (they are shown)
Low intensity mobbing	stay-vocalizing	Vocal	Individual (s) is on a site and vocalizing
High intensity mobbing	approach-vocalizing	Visual, vocal	Vocalizations and movements are constant (they look for the predator), but they do not detect it visually to attack it
High intensity mobbing	attack	Visual, vocal	Direct attack, vocal / visual stimulus was detected and attacked.

Table 1.
Ethogram of potential prey, in response to vocal and visual stimuli of black-and-white owl and collared forest falcon.

during the samplings. Low-intensity mobbing was considered by prey birds when the behaviour of one or more individuals/species changed, mostly due to a vocal response (except for some records where the birds were observing and/or vocalising but remained in the place). On the other hand, high-intensity mobbing was considered from two or more individuals/species and when the recording involved visual, vocal, search, approach and attack behaviours.

2.5 Sampling design

An independent paired experimental design was used to measure the responses before and after applying a single treatment (vocal and visual stimulus), using the organism as its own control. The study was of transversal type, in which we compared the behaviour of different individuals in a determined period [38, 39]. To register the responses of the birds to the predator stimuli, we established four transects [42]. Three transects were 4 km long and one was 3.2 km. Sampling points were established on every route, 400 m apart from each other ($n = 38$). To determine temporal variations (monthly and between the breeding and non-breeding seasons) in the response of potential prey, the sampling period comprised 6 months. In this study, March, April and May were considered as the reproductive season, and June, July and February as the non-reproductive season. We created three categories of bird size: small (10–17 cm), medium (18–21 cm) and large (22–55 cm) [43–45]. All bird species were considered in the analyses, even migratory species. These species are exposed to predators that take advantage of the depletion of these birds [46].

Vegetation and landscape variables were measured in each sampling point and related to behavioural events [47, 48]. The vegetation variables measured were: (a) number of logs, (b) number of live trees, (c) percentage of canopy cover, (d) height of vegetation strata (undergrowth, medium and canopy) and (e) disturbance level of vegetation (with a scale of: 0 = absent, 1 = low, 2 = median and 3 = high). The landscape variables were: (a) distance to roads, (b) distance to dwellings, (c) presence-absence of water sources, (d) presence-absence of open areas (agricultural area, coffee plantation and pastures), (e) land topography (top, valley and slope) and (f) slope in degrees [49].

2.6 Sampling

All behaviours were recorded using focal sampling (i.e. observations of an individual or a group during a determined time). The observations consisted of 9 min at the point of sampling, which allows the detection of several behaviour categories [38, 50]. In addition, we recorded birds performing all behaviours at the time of sampling [39, 50]. Sampling was done in the morning (05:00 to 09:00 h) and evening hours (15:30 to 19:30 h). Each sampling session was 9 minutes, starting with the first 3 minutes in silence to record the presence of any bird species, followed by 3 minutes with an emitted vocalisation of a predator and 3 minutes in silence to record any response [51]. Behavioural events of the birds were recorded during the playing of the vocal stimulus and during the last 3 minutes. The loud-speaker (Radio Shack Power Horn model) used was carried by a second observer, who directed it towards the four cardinal points. In each point, we used visual stimuli [13, 24], which were a plastic owl (morphologically similar to a black-and-white owl) and two-actual size colour photographs of the collared forest-falcon stuck together to have a double view. The plastic owl and the printed image were placed at each sampling point at a height of 6 m above the ground, supported by two tubes with extension.

Pre-recorded vocalisations of the black-and-white owl (at four sampling points) were played during the first 2 h of the morning (05:00 to 07:00) sampling, and at a random point, a different vocalisation (spectacled owl) was played. This was done to avoid habituation of the species to the vocal stimulus [8]. After 2 hours of sampling, the vocalisation of the collared forest-falcon was broadcast, and at one point, the vocalisation of its conspecific, the barred forest-falcon, was issued randomly. The evening sampling began with the broadcast of the collared forest-falcon vocalisation (first 2 hours) and finished with the black-and-white owl vocalisation.

Vocalisations used as stimulus were obtained from Fonoteca de las Aves de Chiapas [52] and xeno-canto (<http://www.xeno-canto.org/>). We used common vocalisations from three different individuals of each of the black-and-white owl, the spectacled owl, and the collared and barred forest-falcons, 3 minutes cut with ADOBE AUDITION CS5.5. ® [53], to avoid pseudo-repetitions [54, 55]. In each sampling point, we recorded the songs or calls of bird species that answered to the stimulus. Recordings were made with a SONY recorder model PCM-M10 with a SONY microphone model ECM-MS907 to identify the bird songs. In addition, a CANON camera model SX530 HS was used to photograph and record the birds' behaviour during or after the stimuli.

2.7 Statistical analysis

Generalized linear mixed models (GLMMs) were used to analyse the frequency variation of the behaviour events, breeding and non-breeding seasons and bird sizes. Behavioural types, months, seasons and bird size were considered as fixed effects, while transects and seasons were considered random effects. For the analysis of similarity between months and breeding and non-breeding seasons, we used the Bray-Curtis index, where 1 means 100% similar and 0 means that there is no similarity [56]. For this analysis, we used the EstimatesS version 9 and InfoStat/E version 2007 program, with a link to the program R 3.3.2 [57, 58].

To determine the relationship between vegetation structural variables and landscape variables with response behaviours of potential prey, we used the binary logistic regression model. The response behaviours were the binary-dependent variables, while vegetation and landscape variables were independent variables. The variables were selected using a combined method of backward elimination and forward selection to obtain the best fit model. We used the coefficient of determination (r^2) to explain the responses of the species in certain sites. The results of the likelihood ratio test were used to explain the weight of each of the variables in the model. This analysis was performed with the JMP-SAS 7.0 program [59]. All statistical analyses were considered significant at $p \leq 0.05$.

3. Results

3.1 Species that responded to stimuli

A total of 596 vocal stimuli of the black-and-white owl and 512 of the collared forest falcon were performed across a total of 528.4 km. We recorded 68 bird species of 12 orders and 28 families, with a total of $n = 574$ response behaviours (Appendix 1). Families with the highest number of responses were Ramphastidae 14% ($n = 81$), Corvidae 13% ($n = 74$) and Tyrannidae 9.5% ($n = 55$). Other families recorded were Tinamidae, Accipitridae and Thamnophilidae. Thirty-eight species (56%) responded to both predators, but at different frequencies. For example, the

long-tailed manakin (*Chiroxiophia linearis*) responded six times to the black-and-white owl and 18 times to the collared forest-falcon. The white-breasted wood wren (*Henicorhina leucosticta*) responded 17 times to the black-and-white owl and seven times to calls from the collared forest-falcon. From the yellow-throated euphonia (*Euphonia hirundinacea*), the fan-tailed warbler (*Basileuterus lachrymosus*), the red-billed pigeon (*Patagioenas flavivirostris*) and the pale-billed woodpecker (*Campephilus guatemalensis*), a single response was obtained to both predators (Appendix 1).

For the black-and-white owl stimuli, 51 bird species belonging to 10 orders and 25 families responded. Four of these species were migratory (olive-sided flycatcher (*Contopus cooperi*), Swainson's thrush (*Catharus ustulatus*), magnolia warbler (*Setophaga magnolia*) and summer tanager (*Piranga rubra*). The species with the highest number of behavioural events was the keel-billed toucan with 13.5% ($n = 37$), followed by the white-breasted wood wren with 6% ($n = 17$) and the mottled owl (*Ciccaba virgata*), collared forest-falcon and gartered trogon (*Trogon caligatus*), with 5% ($n = 14$) each. Thirteen bird species were recorded only once (e.g. yellow-billed cacique, *Amblycercus holosericeus*; fan-tailed warbler; black-faced grosbeak, *Caryothraustes poliogaster*; and yellow-throated euphonia).

The bird responses to the stimuli were individual or of two, three and up to four individuals of the same or different species. The white-breasted wood wren was the species with the highest number of individual behavioural events ($n = 17$), followed by the bright-rumped attila (*Attila spadiceus*) and the blue-diademed motmot (*Momotus lessonii*) ($n = 11$). There were 179 events of individual behaviour (from stay still until to attack); most of the birds only vocalised (129), 16 escaped, 12 vocalised and stayed in one place, 7 stay still (e.g. olive-sided flycatcher, red-throated ant-tanager (*Habia fuscicauda*) and white-breasted wood wren), 7 escaped and vocalised, 5 approached with vocalisations and 3 attacked (i.e. collared forest-falcon, royal flycatcher (*Onychorhynchus coronatus*) and green shrike-vireo (*Vireolanius pulchellus*)).

We obtained 70 response behaviour events with groups of two individuals, of which in 50 events, the birds only vocalised, 10 escaped (e.g. long-tailed manakin, boat-billed flycatcher, *Megarynchus pitangua* and brown jay), 4 stayed in one place while vocalising, 2 escaped while vocalising, 2 approached while vocalising and 2 attacked (e.g. yellow-green vireo, *Vireo flavoviridis*). The species which showed more responses with two individuals was the keel-billed toucan with the highest number of behavioural events ($n = 20$), followed by the brown jay (*Psilorhinus morio*) and the black-and-white owl as an intraspecific response ($n = 8$). We recorded 18 behavioural events with 3 individuals; 6 escaped (3 from red-legged honeycreeper, *Cyanerpes cyaneus* and 3 from green jay, *Cyanocorax yncas*) and 12 vocalised with 3 events each; red-legged honeycreeper, brown jay, keel-billed toucan and masked tityra, *Tityra semifasciata*. We recorded 12 events of behaviour with four individuals; all of them were from the keel-billed toucan; 4 escaped while vocalising, 4 only vocalised and 4 stayed and then vocalised.

There were 12 events recorded of high-intensity mobbing towards black-and-white owls. The bird species were the mottled owl, keel-billed toucan, collared forest-falcon, boat-billed flycatcher, bright-rumped attila, royal flycatcher, yellow-green vireo and green shrike-vireo. We identified seven different behaviours of potential prey of black-and-white owl. Vocalisation was the most frequent behavioural response ($\chi^2_{6,32} = 53.68$, $p < 0.001$; **Figure 2**).

Fifty-five bird species of 11 orders and 27 families responded to collared forest-falcon stimuli. Three of these species were migratory (yellow-green vireo, Swainson's thrush and summer tanager). The keel-billed toucan was the species that had more behaviour events with 14.5% ($n = 42$), followed by the collared forest

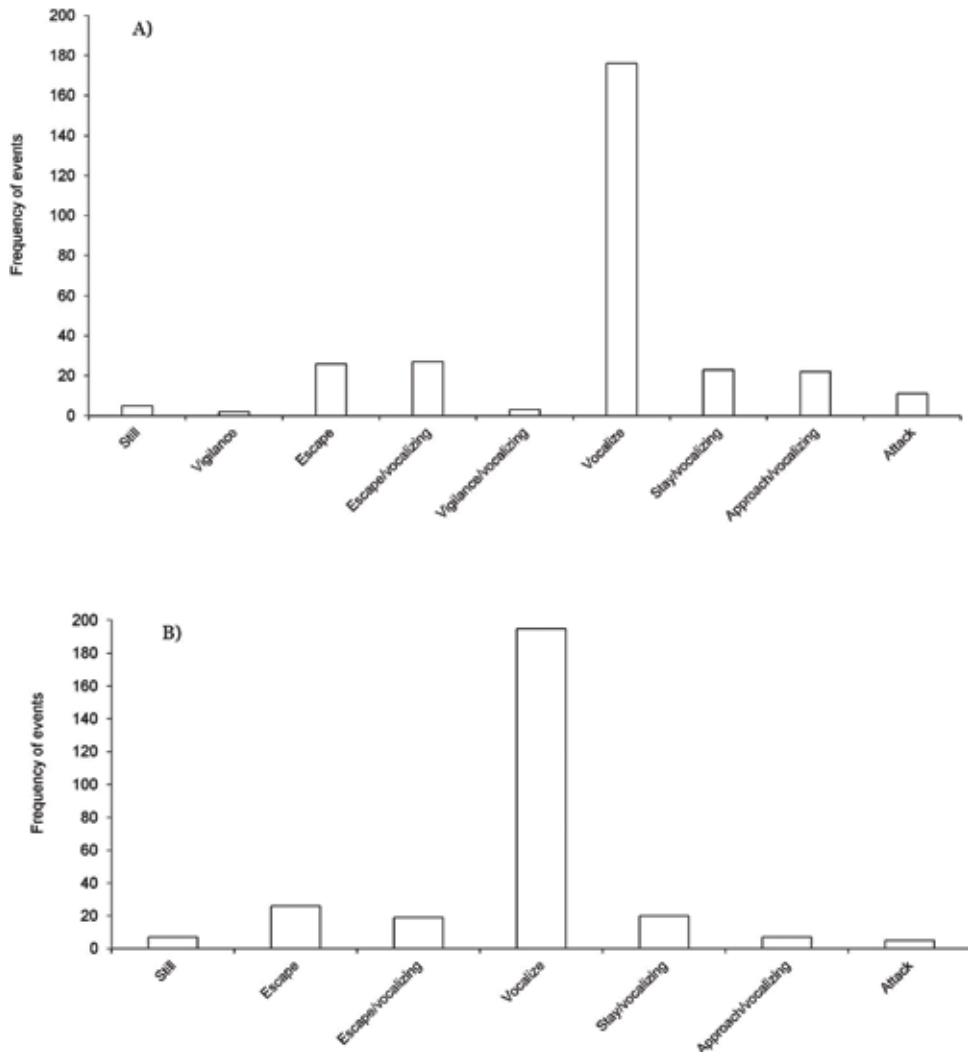


Figure 2.

Frequency of events for each behaviour recorded from potential prey after vocal and visual stimuli of (A) black-and-white owl and (B) collared forest falcon in La Selva El Ocote, Chiapas, during February-July in 2016.

falcon with 9% ($n = 26$), the brown jay with 7.5% ($n = 22$) and the long-tailed manakin with 6% ($n = 18$). Twenty species had only one behavioural event (e.g. fan-tailed warbler, pale-billed woodpecker and ruddy woodcreeper (*Dendrocincla homochroa*), bronzed cowbird (*Molothrus aeneus*) and red-billed pigeon).

The highest number of individual behaviour responses within a species to the collared forest falcon stimuli was interspecific ($n = 20$), followed by the gartered trogon (9), the keel-billed toucan (8), the long-tailed manakin (7) and the social flycatcher, *Myiozetetes similis* (7). We recorded 150 events of one individual response, most of them vocalised (107), 13 escaped, 8 approached vocalising, 6 escaped and vocalised, 6 vocalised and stayed, 5 stay still, e.g. bronzed cowbird, northern bentbill *Oncostoma cinereigulare* and citreoline trogon *Trogon citreolus*), and 3 attacked (i.e. red-throated ant-tanager and social flycatcher). The species that responded in groups of two individuals and had more behaviour events were the keel-billed toucan ($n = 16$) and the green jay ($n = 10$), with interspecific responses (collared forest-falcon; $n = 8$). Sixty-eight events were from 2 individuals, 46

vocalised, 8 approached and vocalised, 6 escaped and vocalised, 4 stayed and vocalised, 2 escaped and 2 attacked (i.e. collared forest-falcon).

From groups of three individuals that responded to the collared forest falcon stimuli, we recorded 54 events, of which 15 vocalised, 15 escaped and vocalised, 9 stayed and vocalised, 6 escaped (e.g. white-tipped dove, *Leptotila verreauxi* and brown jay), 6 approached and vocalised (i.e. white-throated magpie-jay, *Calocitta formosa*) and 3 were vigil and vocalised. The brown jay had the highest response events (12), followed by the white-throated magpie-jay (9) and the keel-billed toucan (9). Three behaviour events were recorded with groups of four individuals; red-legged honeycreeper, plain chachalaca and keel-billed toucan. In this study, we observed only one event of escape from a group of five keel-billed toucans responding to the stimuli of the collared forest-falcon and one of attack from six white-throated magpie-jays. In addition, we recorded 33 high-intensity mobbing events. The species recorded with mobbing were the white-throated magpie-jay, the brown jay, the boat-billed flycatcher and the gartered trogon. Finally, for the collared forest-falcon, we identified nine behavioural responses, with vocalisation being the most frequent one ($\chi^2_{8,36} = 35.07, p < 0.001$; **Figure 2**).

3.2 Similarity of potential prey regarding the frequency of response behaviours and months

Similarity analysis showed that potential preys that responded to black-and-white owl stimuli were 57% similar in March and April (**Figure 3**). In these months, the highest number of behaviour events was observed ($\chi^2_{5,24} = 10.29, p < 0.001$). However, the highest number of species that responded to black-and-white owl stimuli was observed in April and May ($\chi^2_{5,24} = 5.72, p < 0.002$). For the collared forest-falcon, also in March and April, we observed a higher similarity of potential preys with 45%, while in April and June, the similarity was 41% (**Figure 3**). April showed the highest species richness and February the lowest ($\chi^2_{5,24} = 7.09, p < 0.008$). The highest frequency of behavioural events was observed in April ($\chi^2_{5,24} = 12.06, p < 0.001$).

3.3 Frequency of response behaviours of potential preys during reproductive and non-reproductive seasons

Sixty-eight potential prey species responded to black-and-white owl stimuli during the entire study, of which 28 were recorded in both seasons (breeding and

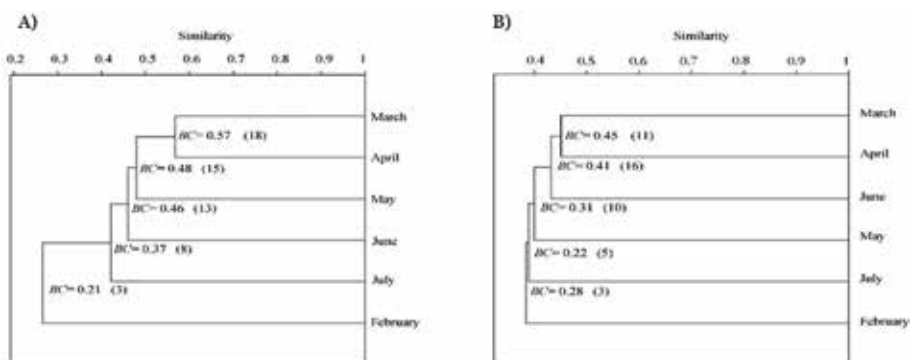


Figure 3. Similarity of potential prey that answered to the vocal and visual stimuli of (A) black-and-white owl and (B) collared forest falcon between months of 2016, in La Selva El Ocote, Chiapas.

nonbreeding), with a similarity of 49%. During the breeding season, we observed the highest species richness and the highest number of behaviour events ($\chi^2_{1,6} = 8.78, p < 0.041$; $\chi^2_{1,6} = 7.34, p = 0.05$). For the collared forest-falcon stimuli, 68 potential prey species responded, and 24 were recorded in both seasons ($BC = 0.508$). Species richness was not different between seasons ($\chi^2_{1,6} = 3.52, p \geq 0.134$), but there were more behaviour events during the breeding season ($\chi^2_{1,6} = 7.24, p = 0.05$).

3.4 Frequency of behaviour events in relation to the size of potential preys

We observed variations in the size of potential preys according to the response behaviours obtained from the vocal and visual stimuli of the black-and-white owl ($\chi^2_{2,12} = 8.29, p = 0.008$). Small species (e.g. social flycatcher, summer tanager, red-crowned ant-tanager *Habia rubica*, bright-rumped attila and masked tityra) showed a higher number of responses than larger species (e.g. pale-billed woodpecker, pheasant cuckoo *Dromococcyx phasianellus*, collared aracari *Pteroglossus torquatus*). For collared forest-falcon stimuli, the number of behaviour events was also different between bird sizes ($\chi^2_{2,12} = 6.91, p \leq 0.015$); it was greater in small species (e.g. royal flycatcher, social flycatcher, boat-billed flycatcher) than in larger ones.

3.5 Vegetation and landscape variables associated with behaviour events

The occurrence of behaviour events in response to black-and-white owl stimuli was associated with the habitat variables canopy height and number of live trees; at the landscape level, the presence or absence of an open area and the presence or absence of a water source were important factors. These four variables were associated in 36% of probability that potential prey could respond to the vocal and visual stimuli of the black-and-white owl ($r^2 = 0.36, X^2 = 15.20, p < 0.004$). For example,

Species	Variables	Estimate	Effect of likelihood ratio
Black-and-white Owl <i>Ciccaba nigrolineata</i> ($r^2=0.36, X^2=15.20, p<0.004$)	Open area	5.89	$X^2=11.61, p<0.0007$
	Canopy height (m)	0.27	$X^2=5.26, p<0.0218$
	Presence or absence of a water source	-12.33	$X^2=3.14, p<0.0762$
	Number of live trees	-0.29	$X^2=1.75, p<0.1857$
Collared- forest Falcon <i>Micrastur semitorquatus</i> ($r^2=0.37, X^2=12.40, p<0.014$)	Canopy height (m)	-0.35	$X^2=5.43, p<0.0197$
	Presence or absence of secondary vegetation	3.24	$X^2=3.99, p<0.0457$
	Number of live trees	0.42	$X^2=2.92, p<0.0873$
	Number of dead trees	0.95	$X^2=3.04, p<0.0808$

Table 2.

Vegetation and landscape variables that influenced a higher probability of recording response behaviours of birds as potential prey for black-and-white owl and collared forest falcon.

our results indicate that in an open area with surrounding vegetation with a canopy higher than 14 m, species will be more likely to respond to the stimuli, and they will also be more likely to respond if there is a lower probability of finding a source of water or live trees with an understory less than 14 m in height (**Table 2**). Four vegetation variables explained a high response event to collared forest falcon stimuli ($r^2 = 0.37$, $X^2 = 12.40$, $p < 0.014$). The variables were secondary vegetation, number of dead trees (stumps and fallen logs), number of live trees (>1 m in diameter) and lower canopy height (<12 m).

4. Discussion

4.1 Response behaviour

In this study, vocalising (predation risk signal) was the highest response of potential prey to both predators. Vocalisation involves energy costs and exposure to predators [60], which vary according to the duration, intensity and acoustic frequency. However, some bird species have developed the ability to transmit vocal signals more frequently to alert members of the flock about the presence of a potential threat [61]. Bird species responded more frequently to vocal stimuli than to visual ones. For example, a bird species' visual detection of a collared forest falcon could be more difficult because it lives inside the forest and is morphologically adapted to hunt inside and at the edges of the forest [33, 62]. Vocal signals or alarm calls can be an adaptation of the prey birds to communicate to other species that an avian predator is nearby.

Species that responded most frequently to vocal stimuli belonged to the families Ramphastidae, Corvidae and Tyrannidae. These species may face potential threats from predators due to their life history traits such as eating habits (feeding in the canopy or the interior of the forest). Species of the families Corvidae (green jay, brown jay and white-throated magpie-jay) and Tyrannidae (boat-billed flycatcher and dusky-capped flycatcher, *Myiarchus tuberculifer*) perform most of their activities in groups, which could make them more evident by increasing encounters with predators [43]. Members of the Tyrannidae family perform behaviours such as watching and escaping to avoid being captured by a predator. We recorded attack behaviour of the royal flycatcher and the social flycatcher and escape behaviour of the boat-billed flycatcher and the bright-rumped attila. Observations of predator species' food habits and optimal foraging show that more abundant prey species are depredated at a higher rate, because the predator minimises foraging time and maximises the energy efficiency [63].

Detecting and emitting signals involve costs (the probability of being found and attacked by a predator) and benefits (increasing survival for the rest of the group) [64, 65]. However, if fewer birds are watching during foraging, this could increase the risk of predation [66]. In this study, bird species as potential prey used vocalisations to help other individuals (in this case escape from the site) or to transmit to the predator that it is willing to combat, even if the cost of this action is death.

We obtained 45 responses of escape to the black-and-white owl stimuli and 53 to the collared forest-falcon stimuli. This type of response has also been observed in the Eurasian blue tit (*Cyanistes caeruleus*) and the great tit (*Parus major*) to a potential threat, consisting of moving between the trees or flying towards the

canopy. If the predator is on the ground, vertical movement may be the safest escape option [67]. In this study, the escape of potential prey consisted of detecting the bird visually, and after the vocal stimuli, the individuals looked around, some moved to a tree, extended their wings and entered into a monitoring mode (moving the head from side to side); they finally escaped among the trees.

The plain chachalaca and the spotted wood quail have been reported to escape into the vegetation and vocalise, but they can also use the attacking behaviour by flying near the vegetation to chase the predator [22]. From our observations in the field, chachalacas, which are noisy by nature, with two or more individuals in one site, respond to any sound that implies a threat by increasing their vocalisations. For pigeons (white-tipped dove, red-billed pigeon and white-winged dove, *Zenaida asiatica*), we identified events of individuals escaping, events of vocalisation, and events where one individual approached and vocalised. Pigeons associated with open areas (i.e. white-winged dove) apparently escape individually or socially by flying fast. However, they may also seek shelter when they are alone and/or under pressure from a predator [22]. Pigeons performed the escape behaviour with individual movements among the vegetation; only the white-winged dove, instead of escaping, approached the visual stimulus and began to vocalise when it was near. Vocalisations indicate that pigeons gave notice to their conspecifics of the presence of the predator, without moving from their shelter.

Woodpeckers responded by moving to the opposite side of the trunk and then escaped the site [22]. We obtained two behaviour events for the pale-billed woodpecker: one escaped and the other only vocalised; in contrast, the lineated woodpecker (*Dryocopus lineatus*) stayed in the place and vocalised, or we only just heard the vocalisation. Species of the Corvidae family may exhibit escape behaviour [22]. However, in this study, six individuals of the white-throated magpie-jay attacked. They were observed foraging on the top of the trees, at about 20 m from the stimuli. When they detected the vocalisation of the collared forest-falcon, they began to vocalise stronger and continuously. They gradually approached until reaching the horn and the visual stimulus of the predator. In this flock, there was an individual who was ahead of the others. The other five individuals repeated the movements of this bird until they identified the visual stimulus and began to attack. We observed 59 behavioural responses to both predators from brown and green jays, including events in which they escaped, escaped and vocalised, vocalised or stayed and vocalised. The behaviour of this family indicates that it frequently has encounters with predators. If these species were close to the stimuli, they were the first to respond by increasing the sound of their vocalisations and moving continuously [22].

Migratory species represented 8% (5) of the total recorded species. Behavioural studies of migratory birds have shown that numerous species defend the transitory or tropical habitat, attacking or chasing other bird species [68]. Most of them may face a greater risk of predation while they are feeding, and it is probably easier for predators to catch them [69]. The anti-predatory behaviour of these birds is the use of vocalisations as warnings by prey birds, which are mostly short and sharp alert calls such as calls of the Swainson's thrush or the summer tanager [68]. Although we recorded behavioural events such as stillness (e.g. olive-sided flycatcher $n = 1$), escape (e.g. Swainson's thrush $n = 6$) and vocalisation (e.g. summer tanager $n = 3$), we consider a greater sampling effort to understand the different types of anti-predation behaviour of migratory species.

Predation is a dynamic mechanism that varies in time and space, in which predators need preys and preys can influence the presence and distribution of

predators. This principle implies that both prey and predator modify their behaviour or morphological features to survive. The result will depend on the specificity of the prey to the predator or of the predator to the prey and may result in population coexistence or decline [9]. Another result would be that predator and prey use search/capture or defence mechanisms, which over time could lead to the divergence of ecological characteristics [70]. The vocal behaviour of bird species in the El Ocote forest could be modified over time, implying new mechanisms in the communication among individuals.

4.2 Similarity of potential prey regarding the frequency of temporal response behaviours

In March and April, we observed most behavioural events for both predators. During the breeding season, males emit vocalisations for courtship purposes that make them more apparent to potential predators, although the benefit of this is to attract their mates or to alienate other males from their territories [9, 71, 72]. Also, in these months, there could be a greater availability of food resources, and therefore, most birds breed during this time; to protect and teach their offspring, they respond to the presence of a predator [9]. In Emilio Rabasa Ejido, prey species showed variations in their responses, the site and the moment where it was detected, so that the presence of a predator influenced foraging decisions of the prey. Species may reduce foraging time to avoid an attack, perform group observations or control group size [64].

The predation mechanism can cause variations in dispersal distances of prey birds during the chicks' care season. Predation events can create a selective advantage for dispersal [73]. Prey species could acquire, through evolutionary time, distinct types of ecological niches that are relatively free of predation pressure to allow their reproduction and survival [70]. Some prey species face a higher risk of predation than others, for instance at sites that are used by predators [69]. However, more studies are needed to understand how prey species face risks of predation during various times and seasons in the year.

4.3 Frequency of response behaviour events in relation to the size of potential preys

Based on the frequency of reported vocal events, we suggest that smaller species are at greater risk of predation than large ones. Small-sized bird species may be easier to capture because they are relatively more abundant than large species. However, it would be important to also consider the vegetation structure, such as the height of the trees in which they feed, combined with exposure to predators, or when species feed in groups [69].

If prey size is similar to their predators, preys would be at a disadvantage when trying to escape because they may have difficulty locating the canopy and could easily be followed by a predator [22, 34]. A lower vegetation density influences which prey can use certain strata of the vegetation. For example, small birds can more often use medium strata and thin branches to escape [22]. For some small species, the strategy of staying in groups has an important advantage such as group young care, social learning for foraging strategies, as well as increased protection and the increased possibility of escaping from a predator [74]. However, individual observation levels in large groups tend to decrease [64, 75, 76]. The cost of monitoring increases in individuals with a high probability of being depredated, such as small species [69]. In this study, small-sized species such as

the red-throated ant-tanager, the masked tityra and the boat-billed flycatcher showed behaviours such as monitoring, approaching and vocalising or attacking the stimulus. This indicates that these species could be depredated by the black-and-white owl and the collared forest-falcon and responded to the stimuli as a defence to a threat.

4.4 Vegetation variables and behavioural events

The probability that a prey responded to the stimuli of a predator was related to the vegetation structure (canopy height and number of live or dead trees) and the landscape (presence or absence of a water source, open area and secondary vegetation) in 36 and 37%, respectively. The arboreal vegetation functions as a shelter for prey against predators, although there are predators such as *Micrastur* species that hunt within the forest [34]. In dense vegetation, medium and large preys could not move quickly, and in the secondary forest, they would find little protection [22]. In territories with dense vegetation, small preys, such as the rufous-and-white wren (*Thryophilus rufalbus*) and the banded wren (*T. pleurostictus*), depend on acoustic rather than visual signals [77].

Birds use sites where they can maximise the diffusion range of their song, although the energy costs of singing and the warning of their presence to the predators are neglected [78]. Vocalisations may increase in environments with dense vegetation, while in open environments, they may decrease. In the first situation, species could be more exposed to intense predation, since predators use hearing to locate their prey [25, 28, 77].

Species of the Trogonidae family live in secondary forests and open areas with scattered trees. They perch in the canopy of the trees and are solitary, although sometimes they form groups for feeding in fruit trees or during the courtship season. However, the gartered trogon is widely distributed in southern Mexico and Central America and tolerates environmental changes. Trogons respond to the presence of owls by emitting sharp and crisp notes and by slowly raising their tails [79]. The black-and-white owl as a potential predator is also associated with secondary forests [45], and vegetation attributes such as canopy height and basal area of trees [69] might explain vocal recognition by prey. Understanding anti-predatory behaviour in birds is important to understand how predators influence ecological systems. Behavioural responses of birds to predation (e.g. stillness, escaping, vocalising and attacking) could be related to the physical structure of the environment; in this sense, the landscape type may influence the risk of predation.

5. Conclusions

Understanding the co-evolution of interacting species is one of the major challenges in the study of ecological systems. For example, studies on interactions between prey and predators and competition for resources should be realized in an ecological time scale comparable to the life of organisms [80]. The ability of birds to use signals is useful for assessing the risk of predation and provides guidelines for understanding bird behaviour, but it is also important

to study the ecological and evolutionary role of predator detection by prey. Results suggest that potential preys modify their behaviour depending on the species, where they are at that moment, the age of individuals, season, climate and previous experiences with predators, creating a behaviour that permits the potential prey to detect or evade a predator. One application of our study in the field of conservation biology and ethology would be to determine connectivity in increasingly fragmented landscapes and to use the behaviour of prey birds and their predators as a model to improve our understanding of this prey-predator mechanism in tropical ecosystems.

Acknowledgements

We thank Carlos Morales and Karla Leal for permissions and logistics during the field work and people in Emilio Rabasa Ejido who helped us during the field work. This work was supported by the National Commission of Natural Protected Areas (CONANP) project PROCER/RFSIPS/27/2015 and ECOSUR. The National Council for Science and Technology (CONACYT No. 573165/565662) provided a scholarship for the first author. We would also like to thank Jack Eitniear and Allen Wootton for helping us with the English revision.

Conflict of interest

The authors declare that they have no conflict of interest.

Compliance of ethical standards

Our study included field auditory and visual detection of 68 bird species in response to 3-minute playback of predator vocalisations. This methodology was used only to collect data for the purposes of this study, and we are aware of the consequences for the reproduction or welfare of the birds. Our research did not require the approval of any Local Ethics Committee in Chiapas, but rather of the Ethics Committee for Research of ECOSUR. The study was carried out in accordance with Mexican legislation and the authorizations given by administrative personnel of the Selva El Ocote Reserve (National Commission of Natural Protected Areas) and inhabitants of the Emilio Rabasa Ejido. Datasets analysed during the present study are available upon reasonable request to the corresponding author.

A. Number of responses of bird species after stimuli (auditory-visual) of two potential predators

The taxonomic classification is based on the list of the American Ornithologists' Union (AOU, 2016).

Order	Family	Scientific Name	English Name	NOM	<i>Ciccaba nigrolineata</i> (No. of responses)	<i>Micrastur semitorquatus</i> (No. of responses)
Tinamiformes	Tinamidae	<i>Crypturellus boccardi</i>	Slaty-breasted Tinamou	A	-	1
Galliformes	Cracidae	<i>Ortalis vetula</i>	Plain Chachalaca		3	5
	Odontophoridae	<i>Odontophorus guttatus</i>	Spotted Wood-Quail	PR	2	1
Columbiformes	Columbidae	<i>Leptotila verreauxi</i>	White-tipped Dove		-	3
		<i>Patagioenas flavirostris</i>	Red-billed Pigeon		1	1
		<i>Zenaidra asiatica</i> ***	White-winged Dove		-	1
Cuculiformes	Cuculidae	<i>Dromococcyx phasianellus</i>	Pheasant Cuckoo		2	2
Accipitriformes	Accipitridae	<i>Rapornis magirostris</i>	Roadside Hawk		-	1
Strigiformes	Strigidae	<i>Ciccaba nigrolineata</i>	Black-and-white Owl	A	13	-
		<i>Ciccaba virgata</i>	Mottled Owl		14	-
		<i>Lophostrix cristata</i>	Crested Owl	A	11	-
		<i>Megascops guatemalae</i>	Vermiculated Screech-Owl		4	-
Trogoniformes	Trogonidae	<i>Trogon citreolus</i> **	Citreoline Trogon		-	1
		<i>Trogon collaris</i>	Collared Trogon	PR	2	2
		<i>Trogon massena</i>	Slaty-tailed Trogon	A	2	-
		<i>Trogon caligatus</i>	Gartered Trogon		14	16
Coraciiformes	Momotidae	<i>Momotus lessonii</i>	Lesson's Motmot		11	8
Piciformes	Ramphastidae	<i>Aulacorhynchus prasinus</i>	Emerald Toucanet	PR	1	-
		<i>Pteroglossus torquatus</i>	Collared Aracari	PR	-	1
		<i>Ramphastos sulfuratus</i>	Keel-billed Toucan	A	37	42
	Picidae	<i>Campyphilus guatemalensis</i>	Pale-billed Woodpecker	PR	1	1
		<i>Dryocopus lineatus</i>	Lineated Woodpecker		1	2
Falconiformes	Falconidae	<i>Micrastur ruficollis</i>	Barred Forest-Falcon	PR	2	-
		<i>Micrastur semitorquatus</i>	Collared Forest-Falcon	PR	14	26
Passeriformes	Thamnophilidae	<i>Thamnophtilus dohratus</i>	Barred Antshrike		-	1
	Furnariidae	<i>Dendrocincla aurobata</i>	Tawny-winged Woodcreeper	PR	3	1
		<i>Dendrocincla homochroa</i>	Ruddy Woodcreeper		-	1
		<i>Lepidocolaptes souleyetii</i>	Streak-headed Woodcreeper		1	-
		<i>Sittasomus griseicapillus</i>	Olivaceous Woodcreeper		3	2
		<i>Xiphorhynchus flavigaster</i>	Ivory-billed Woodcreeper		6	2
	Tyrannidae	<i>Attila spadiceus</i>	Bright-rumped Attila		13	1
		<i>Contopus cooperi</i> ***	Olive-sided Flycatcher		2	-
		<i>Megarynchus pitangus</i>	Boat-billed Flycatcher		3	2
		<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher		1	3
		<i>Myiozetetes similis</i>	Social Flycatcher		1	11
		<i>Oncostoma cinereivirens</i>	Northern Bentbill		8	5
		<i>Ouyechorhynchus coronatus</i>	Royal Flycatcher	P	3	2
	Tityridae	<i>Pachyramphus major</i>	Gray-collared Becard		-	1
		<i>Schiffornis veraepacis</i>	Northern Schiffornis		1	-
		<i>Tityra semifasciata</i>	Masked Tityra		3	6
	Cotingidae	<i>Lipaugus uirrifus</i>	Rufous Piha		2	5
	Pipridae	<i>Chiroxiphia linearis</i>	Long-tailed Manakin	PR	6	18
	Vireonidae	<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike		-	1
		<i>Pachysylvia decurtata</i>	Lesser Greenlet	PR	2	5
		<i>Vireo flavoviridis</i>	Yellow-green Vireo		4	1
		<i>Vireolanus pulchellus</i>	Green Shrike-Vireo	A	4	4
	Corvidae	<i>Calocitta formosa</i>	White-throated Magpie-Jay		-	15
		<i>Cyanocorax yucas</i>	Green Jay		9	17
		<i>Psaltriparus morio</i>	Brown Jay		11	22
	Troglodytidae	<i>Henicorhina leucosticta</i>	White-breasted Wood-Wren		17	7
		<i>Phenopodius maculipectus</i>	Spot-breasted Wren		-	4
		<i>Troglodytes pleurostictus</i>	Banded Wren		-	1
	Turdidae	<i>Catharus ustulatus</i> ***	Swainson's Thrush		6	6
		<i>Turdus grayi</i>	Clay-colored Thrush		2	-
	Fringillidae	<i>Euphonia hirundinacea</i>	Yellow-throated Euphonia		1	1
	Parulidae	<i>Basileuterus lachrymosus</i>	Fan-tailed Warbler		1	1
		<i>Setophaga magna</i> ***	Magnolia Warbler		1	-
	Thraupidae	<i>Cyanerpes cyaneus</i>	Red-legged Honeycreeper		8	9
	Emberizidae	<i>Aimophila rufescens</i>	Rusty Sparrow		-	1
		<i>Arremonops rufivirgatus</i> *	Olive Sparrow		2	4
	Cardinalidae	<i>Caryothraustes polioptera</i>	Black-faced Grosbeak		1	-
		<i>Habia fuscicauda</i>	Red-throated Ant-Tanager		10	8
		<i>Habia rubica</i>	Red-crowned Ant-Tanager		6	5
		<i>Piranga rubra</i> ***	Summer Tanager		2	2
	Icteridae	<i>Amblycercus holosericeus</i>	Yellow-billed Cuckoo		1	2
		<i>Dives dives</i>	Melodious Blackbird		-	1
		<i>Molothrus aeneus</i>	Bronzed Cowbird		-	1
		<i>Psarocolius montezuma</i>	Montezuma Oropendola	PR	-	2
Total of species					51	55
Total of responses					279	295

* Quasiendemic, ** Endemic, *** Migratory; A= Threatened, PR= Special Protection, blank= no category. - No records

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Sustainable Control of Rats by Rodenticide Application and Natural Propagation of Barn Owls (*Tyto Javanica*)

Hafidzi Mohd Noor

Abstract

Rat infestation in crops has been dealt with the crudest method of hunting and trapping to reliance on natural enemies to application of rodenticides and the present approach of IPM by combining baiting with biological control by a suitable predator. Sustainability is the key feature where rat pest is kept below the carrying capacity of the habitat avoiding harming nontarget animals and preserving the environment. Combining rodenticides with predators calls for a balancing act whereby the latter is not exposed in as much as possible to intoxication by the former through secondary poisoning. Long-term exposure to the first-generation anticoagulant rodenticide (FGAR) has given rise to bait resistance, prompting the formulation of highly toxic second-generation rodenticides (SGAR) that may overcome resistance in rat but lead to bioaccumulation of rodenticide residues in the predator leading to lethal or sublethal effects on the latter, which defeats the purpose. Therefore, the choice of rodenticides and applications may bring out the desired effects for a sustainable rat control programme in combination with predators as natural enemies. This paper reports on a number of studies to achieve sustainable rat control programme by combining available rodenticide formulations with the natural propagation of barn owls *Tyto javanica* in oil palm plantation in Malaysia.

Keywords: sustainable rat control, first-generation and second-generation anticoagulant rodenticides (FGAR and SGAR), biological control, the barn owl *Tyto javanica*, oil palm plantation

1. Introduction

Rat infestation is an age-old problem around the globe. Dealing with rat pest in crops or plantation posed a long time challenge that has been tackled over the ages from the crudest method of flushing and hunting [1, 2] to mechanical trapping [3, 4] to translocation of exotic predators or classical biological control [5–12] to the applications of rodenticides of a certain active ingredient or another as a stand-alone or in combination with the propagation of a selected predator [13–18]. However, sustainability is the keyword whereby keeping the rat population below the carrying capacity of the habitat almost indefinitely and at the same time reduces the potential of harming other animals and the environment as a whole.

In agriculture and plantation where food is overly abundant to the depredators such as rodent in this case, keeping the rat population low would be particularly a challenge. Even if a method is improvised whereby huge population of rats is removed at any one time, the turnover rate is incredible that soon the vacant space will be reoccupied in no time, bringing the infestation level to where it originally was. Therefore, to design a sustainable control programme is not straightforward, and one may have to consider a number of options to get the near optimum result. In this chapter, conventional methods of baiting rats with rodenticides will be maintained but in combination with biological control approaches as outlined in the all too well familiar concept of integrated pest management (IPM).

2. Overview of rat control in Malaysia

In the olden days, rat infestation can be described as a plague, destroying whole fields of rice crop ready to harvest. The sight of fallen tillers at day break can be a so heart-rendering sight. Rats seemed to have migrated en masse from someplace else to take advantage of the ripened rice grains. In the 1900s up to the 1940s as per documented, hunting parties involving the whole village were organized to flushed out rats from their burrows and the surrounding areas and actually chasing and beating them as they showed up [19, 20]. Tens of thousands of rats were systematically bludgeoned to death in such campaigns. Despite of the decimation in numbers, there was no guarantee that the population will not be restored or replaced by a neighbouring colony. However, this gave some assurance and a temporary measure for a grain harvest of the season later after the Second World War with the advent of anticoagulant rodenticide; the warfarin became the quick answer to the rat infestation problem. It has remained in the market for decades since, although other more potent and toxic compounds found their way into the market. These classes of rodenticides are fittingly called anticoagulants from their mode of action which induces perforations of the blood vessels leading to massive loss of blood as a result of the suppression of the clotting factor in the blood. They eventually took over the more acute poisons with almost immediate effect upon consumption such as zinc phosphide. Although the application of the latter has been made unlawful, farmers are known to still subscribing to it and other unspecified compounds. Applications of the warfarin or what was eventually labelled as first-generation anticoagulant rodenticides (FGARs) have led to resistance as a consequence of prolonged exposure of the rat population over an extended period [21, 22]. Over-reliance of the warfarin has been attributed to the phenomenon of commensal rats in urban areas as well their agricultural counterparts, developing high tolerance and even complete resistance to the former [23, 24]. Not only warfarin has been made ineffective; rats are also not succumbing to other FGARs compounds perhaps by way of cross resistance. These have prompted the chemical companies to develop second-generation anticoagulant rodenticides with potency or toxicity that may reach 10fold compared to FGARs. Compounds such as bromadiolone and brodifacoum have been in the market for a reasonably long time that it is anticipated that rats will eventually overcome them as a result of long-term exposure. Apart from being highly toxic, which may expedite the development of resistance, they are also harmful to the other creatures which may consume the bait or the predators that become exposed to the compound indirectly by feeding on the prey. Indirect feeding may also involve a secondary or a top predator consequently causing tertiary poisoning. The residues of the active ingredient will build up the food pyramid or down the food chain, accumulating in the tissues and vital organs in the process. The end or top predator will bear the brunt as the bioaccumulation of the residues has reached a level that is

fatal [25–27]. Another more destructive impact is the sequestration of the residues on the eggs through the process of ovulation, leading to lower fecundity, addled eggs, lower clutch size and smaller less healthy brood [28, 29]. Many raptors in the temperate regions have become extinct in certain parts of their geographical distribution in Europe and North America [30]. Therefore, unsustainable rodenticide application has a huge impact on the wildlife at the end of the food chain [31]. Thus, to redeem the situation and reclaim our natural ecosystem, a more benign approach has to be discovered to replace the standard conventional rat baiting method.

3. Biological control of rats in oil palm

Resorting to biological control would be the method of choice as predators would keep prey population in check. In a natural environment where the ecosystem has reached an equilibrium, the population of prey and predator dynamics would always be in tandem [32–34]. This would lead to a stable relationship as there would not be cycles of trough and population crash as a result of over predation. Such an ideal association may be possible in a natural habitat where the vegetation and food resources limit the population size. The carrying capacity of the habitat for any particular prey and in turn predator would always be in keeping with the availability of resources which is heterogenous for the most part. In a monocropping situation, there is an overabundance of a particular resource to a handful of consumer species which are best to adapt and exploit the resources. As a consequence the carrying capacity of these handfuls of species may explode by several folds compared to the more heterogenous natural habitat. This in turn will bring about huge crop and economic losses. The predators may be incapacitated to deal with such high density of prey and may not be able to grow in population size to match the prey availability [35]. After all food limits not only the population density of the prey but also the nesting sites and foraging space. Therefore, the lower number of predators than what the habitat can actually support will only harvest a fraction of the surplus individuals of prey [36, 37]. This will only sustain an exceptionally high prey density which translates into high volume of crop damage. Therefore, identifying a suitable predator for a rat prey would have to take into consideration the adaptability and the carrying capacity of the habitat of the said predator.

Small mammals such as rodents would be the prey choice for most medium size predators like civet cats, mongoose, monitor lizards, the more agile snakes and birds of prey [38–47]. These resident predators casually prey on rats apart from other invertebrate prey, amphibians, small reptiles and mollusc. The varied prey is suitable for a forest habitat that is home to a myriad of invertebrates to compensate for the scarcity of rodents and larger prey which are occasionally present. Some of these animals also sample roots, tubers, fruits and other plant matter. The diet structure may not be suitable for candidacy of a biological control agent. The feeding capacity may not fulfil the criteria for an effective predator of the prey. Furthermore the range of food of such predators makes them less than ideal to be recruited as a biological control agent. Snakes and reptiles in particular have a lower food requirement by virtue of its poikilothermic nature. It may not require as much food to sustain its metabolism. Therefore, they consume less food and remove fewer prey than homeotherms.

4. The role of raptors

Birds of prey or raptors especially eagle are day hunting predator. Although the diet of eagles may consist of a range of prey, they are predominantly small

mammals such as rodents. However, rats are nocturnal animals, and in terms of temporal distribution, the prey and predator are not compatible. Therefore, eagles and the like are out of the question. Having discounting the eagle and allies, the owls on the contrary are nocturnal birds of prey. They are active from dusk to dawn, and their eyes and habits are designed for hunting rodents in the cover of darkness. There are two types of owl: the true owl and the barn owl. In Malaysia and Indonesia, the two largest oil palm producers in the world, many wildlife have become adapted to inhabit and forage for food. Owls particularly barn owl has become a common resident especially where artificial nest boxes are provided. In those plantations where artificial nest boxes have been established, the barn owl population has grown considerably to effectively deal with rat infestation, especially in combination with a suitable rodenticide bait.

5. The barn owl *Tyto javanica*

The barn owl *Tyto alba* is believed to have arrived at Peninsular Malaysia from the island of Java, perhaps at the turn of the century based on the first documented observation [48]. The first recorded breeding was documented in Johore in 1969 [49]. A vagrant species, the barn owl has a worldwide distribution except for Antarctica where it is absent as well as the remote atolls in the Pacific. It is associated to farm and agriculture landscape, where it typically seeks refuge or nest in barns and other farm buildings. While barn owl is a common sight in the fields and natural landscape of Europe and North America, it is not common in the agricultural landscape of Malaysia. Rice farmers were not familiar with the owl prior to the late 1980s, whereby they were first introduced by the Department of Agriculture as part of the rat control programme in the ricefield in the state of Selangor and Perak [50]. The infrastructure which largely consists of concrete buildings may not be suitable as refuge for owls. Therefore, artificial nest boxes were installed which boost the local owl population. A year after the implementation of the programme, crop damage as a result of rat activities has dropped considerably from around 10–15% to less than 2% [15]. The damage levels were maintained at that low level for 5 years straight and gradually increased to around 5% which was attributed to the dilapidated condition of the nest boxes. They were made of plywood and apparently were not durable and no longer habitable. Not only the lower crop loss was substantially lower, rat baiting was cut down from eight to just a single round per season. With only two baiting rounds necessary per year to bring down the base rat population lower than the carrying capacity of the ricefield habitat, so that the owls can suppress the population turnover rate, the economic benefits are tremendous.

6. Rat infestation in oil palm

Barn owl programme in the ricefield was actually preceded by a pioneer programme in the oil palm. Oil palm was first grown in the country in 1917 and cultivated on a commercial scale in 1950. Unlike in its original home where it grows naturally, in Malaysia oil palm is a cultivated crop with a high productivity. The release of the pollinating weevil *Elaeidobius kamerunicus* on a large scale has pushed the palm oil production to unprecedented levels. The oil palm fruit bunch provides nutritious food source for birds and small mammals, particularly squirrels and rats. Squirrels particularly the plantain or red-bellied squirrel *Callosciurus notatus* and the grey squirrel *Callosciurus caniceps* are common in oil palm plantation [40, 51]. While the squirrels sample the oil palm fruitlets nibbling away its rich

mesocarp and kernel during the day, rats feed on them at night [52]. In the early stage, these rodents may visit oil palm plantations especially those that are contiguous with the natural forest to feed and return back to their natural habitat where they breed and forage. However, with these rodents particularly rat with a high learning capacity and adaptability, they eventually adopt the oil palm plantation as home. The first rat species that is known to adapt successfully in the oil palm plantation is the wood rat *Rattus tiomanicus*, which originally live in the shrubs and secondary forest [53]. When they start to nest in the spaces within the bases of the oil palm fronds, the oil palm plantation is the new adopted home for *R. tiomanicus*. Thus, it is now by and large associated with oil palm [54]. With the high availability of such nutritious food, the carrying capacity of the crop for rat was estimated at over 350 rats per hectare. In its natural habitat where food is scarce and with diverse niches which support more species of small mammals, the interspecific competition is greater [3, 4, 46, 47, 55]. Thus, the population density of *R. tiomanicus* can be manyfold higher than its original natural habitat. Losses attributed to *R. tiomanicus* and other rat species to a smaller extent can reach anywhere from 5% up to 30% or even higher in some situations [56].

In areas where oil palm plantation is adjacent to the ricefield, the common rat species found is the ricefield rat *Rattus argentiventer*. In that situation *R. argentiventer* is the dominant species, but studies have shown that its presence is transient, i.e. up to 4- or 5-year-old stand only. Other rat species may take over such as *R. rattus diardii*, which is common in areas near human habitation or *R. tiomanicus*. At any rate, the rat density hovers from 200 to 400 individuals per hectare. Damage is confined not only to the fruitlets but also to the apical bud at the nursery and young planting stage [56–59]. At 30–36 months when the young oil palm starts to crop, while the crowns are low lying, damage can be severe on the fruit bunches. Rats may also devour the male and female florescence, and they may also feed on the larvae of the pollinating weevils, reducing the fruit set. Recently invasion by a much larger species the bandicoot rat *Bandicota indica* in plantation in the northern state of Perlis showed that not only do they completely devour the florescence but they also feed away the base of the outer frond of young palms, killing them in the process [59].

The frequent use of rodenticide which has been the mainstay of rat control in oil palm has led to some serious implications to the ecosystem. The most direct consequence is the unintended poisoning of nontarget species especially wildlife. Since rodenticides are all broad-spectrum, it is fatal to any mammals of birds which casually consume them. As the rodenticides are presented as baits, they are likely to be picked up by wildlife including forest rat species which lives near the forest edge and may undertake daily foraging inside the plantation. Apart from primary exposure, predators or scavengers can be duly exposed to secondary poisoning from feeding on prey or carcass that has succumbed to the effects of the rodenticide [60–65]. Bioaccumulation of the active ingredients may lead to long-term sublethal effects or immediate lethal effects [66–69]. Another implication which is counterproductive is the development of resistance individuals as a result of natural selection against rodenticide toxicity. It will eventually give rise to a population which is predominantly resistant, and the susceptible individual will systematically disappear over time [70, 71]. In such a situation, the rodenticide will be rendered ineffective, and a more potent rodenticide will have to be synthesised to overcome the resistant individuals. There is a possibility that resistant individuals will exhibit cross resistance to a range of other rodenticides of different active ingredients.

In the oil palm plantation, as a result of a long-term application of warfarin, a first-generation anticoagulant rodenticide has led to many rat populations which turned resistant, prompting planters to switch to brodifacoum, a second-generation anticoagulant rodenticide (SGAR) introduced in the early 1980s [72].

7. The use of barn owl for rat control in oil palm

Therefore, biological control using predators is the closest to depict nature. However, the capacity or predation rate will have to keep with the prey population density [8, 35]. Predators may act in a numerical fashion, i.e. increase in prey will bring about increase in predation rate. This can be realised theoretically by higher rate of hunting and consumption by an increase in predation numbers [73]. This can be achieved by either increasing production rate or higher immigration rate to take advantage of the higher prey density. Naturally this is difficult to achieve because there is a lag time for the predator numbers to keep up with the prey population. The consequence is higher crop damage before the predator can decimate the prey. The other responses of the predator can be functional, i.e. each individual predator increases its consumption on that particular prey species [74, 75]. Theoretically this is applicable, but in reality, the prey species may not be varied which is ideal for a generalist predator which simply switches prey type based on availability [76]. In a situation of a crop habitat where there's only one common species, it is impossible for the predator to modify its diet unless it immigrate or emigrate depending on the availability of the single prey type. These are the theoretical consideration when choosing a natural enemy to be recruited for an effective biological control programme for rats in oil palm [77].

The barn owl seems to be an ideal predator given the circumstances in the oil palm plantation [78]. It does not build its own nest. Natural potential nesting sites such as the hole in a trunk is next to impossible to come by. Thus providing artificial nest boxes which the owl readily occupies boosts numbers to match with the rat infestation levels. With the huge prey availability, nest boxes not only increase breeding pair to take up residence and breed; the reproductive level can increase to take advantage of the food availability. The clutch size that ranges from typically 4 to 7 is dictated by prey availability [10, 66, 78–80]. A clutch size of 10–12 eggs is documented during peak season of the rat prey. This is apparent particularly in the ricefield during the land preparation stage after harvesting where the subadult rats born of the season start to join the aboveground population [81]. They guarantee a good supply of food for a high brood size or owlet numbers of the season. The owls have a self-checking mechanism to regulate their population size. In times of low prey numbers, the clutch size is smaller to sustain most of the chicks. When food is particularly scarce, the chicks will be subjected to differential survival. Since the egg hatches asynchronously, i.e. at intervals of 2 to 3 days, the size of the chicks from the same brood is different. In fact there is a gradation in size or height of the chick from the largest to the smallest [10, 78]. In unfavourable season only the larger owlets will get sufficiently fed to grow to fledglings. The smaller ones will starve to death by virtue of not being able to compete for food with the larger siblings. Fledging success is typically high in the region of 80% unless owl population is subjected to application of highly toxic rodenticide in the environment [66, 78]. There has also been cannibalism, i.e. owlets being killed by the respective parents, and this behaviour may be triggered by insufficient food. In a way this is a mechanism that leads to a numerical response of sort.

The high rate of prey removal which is not necessarily translated into prey consumed is another attribute of the barn owl. The male barn owl which has been observed to bring prey to the nest may take home more prey than what is necessary to feed the chicks. In many occasions the carcasses were left to rot in the nest boxes, and only a fraction of the prey was actually consumed. This is an added advantage as it increases the kill rate more than the daily food requirement. From casual survey in the fields, the number of rats removed from the fields by a breeding pair of barn owl is in the region of 800–1500 rats per breeding season. Thus, by having an optimum density of nest boxes in the plantation, barn owl can bring down rat numbers substantially.

However, the prolificity of the rat population leads to a high turnover rate which the owls cannot keep up. Thus, the baseline population of the rat needs to be lowered by the application of rodenticides. Barn owl in combination with a suitable rodenticide will bring about the desired effect, i.e. sustainable rat management in oil palm.

Barn owl has many of the attributes of owls which make them excellent nocturnal predators, features like the binocular vision and the almost complete 360 degree of the head turn. However, it lacks the feature of the more secretive owl, the typical owls. The barn owl relies on keen hearing more than eyesight, especially when hunting in the thickets and forest undergrowth. The differential positioning of the ear cavity enables the owl to detect its prey with near precision. Thus, the barn owl can hunt in darkness and rely on the sound made by a potential prey as the cue. The wing area to body weight ratio is particularly larger than most birds, so that it does not have to flap harder to create lift causing a lot of air turbulence. The owl only needs to glide effortlessly and strike at its unsuspecting prey.

The features that make the barn owl close to an ideal predator have prompted efforts of translocating owls to areas that are not known to have a local resident population [82]. Several attempts have been made to translocate owls from the Peninsular Malaysia to Sabah and Sarawak. There has been some spectacular success in this venture. Even though the oil palm landscape may not be similar with that in the Peninsular, with varied different species of rats abound, the translocated owls have established well and been breeding successfully [83]. In Lahad Datu, Sabah, owl's translocation programme that started with ten pairs of owl in 2015 has grown to a population of more than 700 individuals [84, 85].

8. Sustainability of application of biological control using barn owl

Since barn owl is a generalist predator and responds to prey availability by numerical response, i.e. increasing fecundity or immigration/emigration, the effectiveness as a natural predator of rats in the long run relies much on the prey/food supply [86, 87]. Since, in many occasions, infestation of rats in oil palm plantation has reached epidemic levels, the reliability of the owls may not fulfil the control requirement. There was an abundance of prey that only surplus individuals of the aboveground population will be harvested [35]. The infestation status will remain above the economic threshold or crop injury level. Therefore, the application of rodenticide has to be placed in combination with the barn owl programme. Warfarin as the classical FGAR has been applied in combination with barn owl propagation since the 1970s and well into the 1980s. Past studies have assumed warfarin has no apparent effects on barn owl fecundity and population status. When rat has shown evidence of resistance and plantations gradually or abruptly switched to SGAR particularly brodifacoum, barn owl population in a number of occasions experience a sharp decline or were completely wiped out [72]. The susceptibility of owls to the effects of bioaccumulation of SGAR residues in the vital organs and tissues has rendered the combination of the latter with rodenticide futile [63, 66, 88, 89].

The impact of FGARs may not be apparent in terms of immediate lethal effects. Studies on sublethal effects measured in terms of lowered nest occupancies, fecundity, lower brood size and lower fledging success have shown that FGARs can have some long-term effects on the viability of the barn owl population. It may lower the fitness of the individuals and eventually the population as a whole [90, 91]. A study investigating the sublethal effects of anticoagulant rodenticides in an oil palm plantation in Pahang, Malaysia, over four breeding seasons has indicated that FGARs like chlorophacinone lead to lower nest boxes occupancies, significantly lower brood size and lower fledging rates (**Table 1**). However, the result from the bromadiolone (SGAR)-treated area was significantly lower than chlorophacinone in terms of nest

occupancy [92]. Another study in oil palm in Perak suggested that the brood size and the fledging rate were lower in brodifacoum (SGAR)-treated plot than warfarin (FGAR)-treated plot which in turn was lower than the untreated plot (Table 2) [66].

Low mean fledging rates of 2.65 and 2.20 in chlorophacinone (FGAR)- and bromadiolone (SGAR)-treated areas, respectively, suggest that owls are at considerable risk in maintaining a stable population. The nestlings were most likely to have succumbed to the toxic effects during their development stage. Similarly low fledging rates of 1.52 and 0.50 were recorded in the warfarin- and brodifacoum-treated plots, respectively. Henny [79] estimated that 1.9–2.2 fledging per breeding pair is the minimum reproductive rate to maintain a stable barn owl population. Based on these results, chlorophacinone and warfarin (FGAR) may not differ much compared to bromadiolone and brodifacoum (SGAR) as far as the long-term survival of owls for a sustainable rat control programme.

	Bromadiolone	Chlorophacinone	Rodenticide free
Occupancy	37.20 ± 1.14 ^a	51.79 ± 1.34 ^{bc}	83.33 ± 3.60 ^c
Clutch size	3.56 ± 0.10 ^a	3.69 ± 0.10 ^a	4.69 ± 0.11 ^a
Brood size	3.11 ± 0.06 ^a	3.38 ± 0.07 ^a	4.21 ± 0.12 ^b
Fledging rates	2.20 ± 0.10 ^a	2.65 ± 0.06 ^a	3.95 ± 0.07 ^b

Values in rows with different letters are significantly different ($P < 0.05$).

Table 1.

Occupancy rates, clutch size, brood size and fledging rates (mean % ± S.E) of barn owls in Pahang, Malaysia.

	Brodifacoum	Warfarin	Rodenticide free
Clutch size	4.83 ± 1.64 ^a	3.95 ± 0.68 ^a	5.43 ± 1.07 ^a
Brood size	2.06 ± 1.42 ^a	2.17 ± 0.80 ^b	4.21 ± 0.12 ^c
Fledging rates	0.50 ± 0.17 ^a	1.52 ± 0.73 ^b	4.40 ± 1.01 ^c

Values in rows with different letters are significantly different ($P < 0.05$).

Table 2.

Clutch size, brood size and fledging rates (mean % ± S.E) of barn owls in Perak, Malaysia.

	Bromadiolone	Chlorophacinone	Rodenticide free
Wing length (cm)	26.02 ± 0.22	26.30 ± 0.23	28.70 ± 0.14*
Weight (g)	544.4 ± 7.05	565.0 ± 8.44	579.9 ± 10.07*

*Wing length and weight of barn owls in rodenticide free area were significantly longer and higher to barns owls exposed to bromadiolone and chlorophacinone.

Table 3.

Mean wing length of barn owls exposed to bromadiolone (SGAR) and chlorophacinone (FGAR) in Pahang, Malaysia.

	Brodifacoum	Warfarin	Rodenticide free
Wing length (cm)	22.15 ± 0.23	25.86 ± 0.13	26.28 ± 0.11*
Weight (g)	554.9 ± 8.72	585.8 ± 6.62	613.3 ± 5.98*

*Wing length and weight of barn owls in rodenticide free area were significantly longer and higher to barn owls exposed to brodifacoum and warfarin.

Table 4.

Mean wing length of barn owls exposed to brodifacoum (SGAR) and warfarin (FGAR) in Perak, Malaysia.

Nestlings in the rodenticide-free plots show the longest wingspan and greatest body mass compared to the SGAR- and FGAR-treated areas in both Pahang and Perak (**Tables 3 and 4**). The reduction in wing length and body mass ranged from 10 to 16% to 7–10% from the sublethal effects of SGAR and 2–8% to 6–10% from the sublethal effects of FGAR, respectively. There were teratogenic signs in a few nestlings exposed to brodifacoum as a morphological evidence to support claims of secondary poisoning. Nestlings raised in rodenticide-free area fledged successfully upon release into the field, but those from treated areas need another 1 or 2 weeks before they can take to flight [66].

9. Conclusion


The barn owl is an effective biological control agent on rats. However, its natural or facilitated rearing by providing nest boxes in combination with rodenticide can have long-term sublethal effects on the former. The choice of rodenticide is crucial to sustain owl population in oil palm. SGAR can have a greater implication in terms of lowered fecundity and morphological impairments. However, the sublethal effects of FGAR only differ in terms of scale compared to that of SGAR. Therefore, baiting strategy and botanical-based or biological rodenticide need to be formulated for a sustainable rodent control with barn owl.

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A Review of European Owls as Predators of Bats

Alan Sieradzki and Heimo Mikkola

Abstract

Fossil evidence indicates that owls have been preying on bats from as far back as the Pleistocene. Overall, bats form quite small portions (i.e. trace to 0.2%) of the diets (by prey frequency) of European owls. An assessment of dietary studies and anecdotal accounts reveals that five species of European owls, the Eurasian scops owl *Otus scops*, Pygmy owl *Glaucidium passerinum*, Tengmalm's owl *Aegolius funereus*, little owl *Athene noctua* and Ural owl *Strix uralensis*, rarely feed on bats (with less than 0.1–0.4%) and a further two species, short-eared owl *Asio flammeus* and eagle owl *Bubo bubo*, may only take bats occasionally, while three species, long-eared owl *Asio otus*, barn owl *Tyto alba* and tawny owl *Strix aluco*, feed on bats more frequently. In this study, a total of 19,864 recorded bats have been preyed upon by these owls, with as many as 48 bat species being identified. Barn and tawny owls have captured most of this total (47.1 and 41.9%), followed by the long-eared owl (7.6%), while short-eared and eagle owls take similar amounts of bats (1.1 and 1.7%, respectively). Owl predation on bats deserves future research because it may help contribute to our knowledge on bat biodiversity and distribution and possibly identify an additional risk for small populations of endangered bats.

Keywords: European owls, bats, predation

1. Introduction

Bats are the only mammals capable of self-powered flight yet constitute some 20% of all living mammal species, with as many as 110 separate bat species coexisting within the same ecological community, a number that far exceeds that of any other mammalian group [1, 2]. Bats diversified in the Early Eocene in response to an increase in prey diversity, and Eocene bat fossils have been found on most continents leaving the geographic origin a source of debate [1]. Despite their taxonomic and ecological diversity, modern bats (order: Chiroptera) are almost exclusively nocturnal. Rydell and Speakman [3] think that predation risk could have been a significant factor preventing early bats from becoming diurnal. The only other vertebrates that exploit niches for nocturnal flying predators are the owls and nightjars. Fossil evidence indicates that owls have been preying on bats from as far back as the Pleistocene [4, 5]. Since bats are very fast in flight, predation pressure on bat populations is likely to be a minor cause of mortality. Indeed, in the owl diets from North America (23,888 prey items) and temperate Europe, plus Iraq, reviewed by Marti [6], bats did not occur. In later reviews, Mikkola [7] found that bats accounted for 0.04% of prey items of barn *Tyto alba*, tawny *Strix aluco* and long-eared owls *Asio otus* in the British Isles (67,405 prey items) with the same percentage

for short-eared *Asio flammeus* and Tengmalm's owls *Aegolius funereus* (15,147 prey items) in Europe and Finland. For the Eurasian eagle owls *Bubo bubo* (17,615 prey items), bats accounted for 0.03% of prey taken in Fennoscandia.

In this paper, we examine the ecological relationships between owls and bats and see if the larger owl species take larger bats as they tend to do with other prey [8].

2. Methods

We conducted a literature review examining bats as prey in the diets of European owls. The literature examined was published between 1886 and 2018 and covered the ecological timeframe of the Pleistocene to current day. A total of 1680 publications were examined, and a synthesis of the findings is reported here. Utmost effort has been made to avoid duplication in the counting of the same bats mentioned in the review papers and/or multiple papers by the same author. The collection of the data was limited to Eurasia and one particular case study in North Africa (short-eared owl—Algeria). Only 8 European owl species had more than 10 bats in their diet studies, namely, barn owl, tawny owl, long-eared owl, short-eared owl, Eurasian eagle owl, Tengmalm's owl, Ural owl *Strix uralensis* and little owl *Athene noctua*.

Bat weights are drawn from [9–13] as an average of values given. Species weight is the average of the species of that family. Owl weights from [14] are an average of extremes for females and males combined. Our analysis is focused on the frequency of bats in the diet of owls; we also compare the weights of the bat species to the weights of the owl species which ate them. We did not assess bats in terms of their role in the collective biomass of prey taken by the owls.

3. Results

3.1 How owls capture bats

Bats are captured by owls mainly during the periods of emergence or return from roosts, but owls are in general not well adapted for catching bats [15]. The relative benefits of capturing substandard individuals are greatest just when a predator is attacking a species of prey which is typically difficult to capture and kill [16].

Some authors have indicated that barn owls frequently capture young bats that are not yet able to fly [17] and that bats seem to be rarely captured in flight [18]. In Vickery Bat Cave, Oklahoma, barn owls were observed using a wholly unique technique to capture adult Mexican free-tailed bats *Tadarida brasiliensis*. Appearing at dusk when the bat flight from the cave was at its height, the owls dropped from a ledge only 3 m or so above the bats and moved swiftly along with them, often making a capture. Each owl appeared to select one bat before starting the chase, and the bats were caught with 'unerring precision.' Looney [19] witnessed on one September evening the capture of seven bats by one or more owls within a 45-minute period.

Another technique witnessed at a different location [20] was when a barn owl flew into a column of bats head-on from above, stalled, with head up, feet down and wings spread wide, catching a bat that struck it in the chest. It was assumed that the bats were not using their echolocation apparatus while flying in such a dense mass. The owl was observed to make four successful captures using this technique.

Research of Petrželková et al. [15] indicates that barn owls most probably prefer to prey on volant inexperienced yearling bats which are easier to catch while

reaching almost adult size. Yearling bats lack flying skills, they are conspicuous during the emergence, and they often concentrate near the roost during their early practice flights, making them more vulnerable to owl predation than adults.

Spitzenberger et al. [21] recorded, with an infrared camera and an automatic registration device, tawny owl attacks on bats entering an attic roost through an access window. At least 333 *Myotis emarginatus* bats entered the roost by flying over or past the owl which attacked 252 times but with only 31 strikes being successful. During a successful attack, the owl extended its legs, jumped upwards with raised wings and snatched and killed the entering bat with the talons of the foot, tore it apart and ate it on the spot or carried it away. The owl killed 5.3% of the maximum number of female bats roosting in the attic during 12 nights. By restricting its attacks to the period of late pregnancy, the owl took advantage of the state of highest vulnerability of the female bats in this maternity colony.

The observations of [19–21] would suggest that individual owls develop their own unique techniques for capturing bats on the wing.

Bats also seem able to avoid predation to some extent during their evening emergence and morning return to and from the roost. Güttinger [22] noted that *Myotis myotis* changed their emergence exit from a roost to avoid the attacks from tawny owls. Petrželková and Zukal [23] have shown with the use of a trained barn owl that *Eptesicus serotinus* bats are using clustering during emergence as an important anti-predation strategy although the owl presence did not induce any major changes in other measured parameters (like onset, end, rate or duration of emergence).

Boratyński [24] made an interesting observation in Poland on how a tawny owl was attempting to catch a *Nyctalus noctula* in the air, but the bat ‘hid in the predator’s shadow’ by flying very close behind it and waiting until the owl gave up hunting. Finally, the bat flew away safely after the owl ceased searching for the lost prey.

Forest-dwelling owls may experience difficulties in capturing any bats that are present, as bats tend to fly close to the trees, as the study by Russo et al. [25] suggests. This may explain why both the great grey owl *Strix nebulosa* and the hawk owl *Surnia ulula* have so far had no bats in their diet lists; and the extremely well studied Eurasian Pygmy owl *Glaucidium passerinum* has so far been recorded preying on only one *Myotis daubentoni* and one unidentified Vespertilionidae bat in Finland [26] and another in Russia [27]. Scherzinger [28] was wondering why *Plecotus auratus* is not found in the diet of the Pygmy owl as both species are known to use old *Dendrocopos major* holes.

3.2 Owl species and bat diversity

At least 48 bat species have been identified in the diet of eight Eurasian owl species (**Table 1**). A total of 19,864 bats have been preyed upon by these owls. The barn owl has captured 47.1% of all recorded bats in this review, but the tawny owl comes a close second with almost as high a percentage (41.9%), although its food samples have been studied much less than those of the barn owl (well over 5 million prey items). The long-eared owl comes far behind these two with just 7.6%. The short-eared owl and the eagle owl take similar amounts of bats (1.1 and 1.7% from this material, respectively). With only trace amounts of bats in their diets (i.e. 0.4 to 0.1%), we still list the little owl, Tengmalm’s owl and Ural owl in **Table 1** but the scops owl only in **Table 2**.

It has been said that larger owl species take larger prey [8]. This study shows, however, that all sizes of bats are widely represented in the diet of the studied owls (**Table 1**). However, there is a statistically significant correlation in the weight of eaten bats and the weight of the owl (0.736, $p < 0.05$). The heaviest owl *Bubo bubo* takes bats with an average weight of 21.5 g, while the smallest owl *Aegolius funereus*

Bat species and weight in grams	<i>T.a.</i>	<i>S.a.</i>	<i>S.u.</i>	<i>A.o.</i>	<i>A.fl.</i>	<i>B.b.</i>	<i>A.fu.</i>	<i>A.n.</i>	Total
<i>Pipistrellus pygmaeus</i> 5.1	50								50
<i>P. pygmaeus</i> or <i>P. pipistrellus</i> 5.3	36								36
<i>Pipistrellus pipistrellus</i> 5.5	661	2415		5	1	10		8	3100
<i>Myotis mystacinus</i> 6.1	69	205	1	2		8	5	2	292
<i>Myotis brandtii</i> 6.5	16	151				1			168
<i>Pipistrellus abramus</i> 6.5			1	658					659
<i>Murina huttoni</i> 6.7		1							1
<i>Rhinolophus hipposideros</i> 6.9	69	135		1		2			207
<i>Pipistrellus</i> sp. 6.9	145	1		144	7			7	304
<i>Murina hilgendorfi</i> 7.0				4					4
<i>Pipistrellus kuhlii</i> 7.3	2146	21		113				12	2292
<i>Hypsugo savii</i> 7.5	16	3						1	20
<i>Asellia tridens</i> 8.0	36			13		3			52
<i>Myotis nattereri</i> 8.3	523	71		13		4	3	1	615
<i>Myotis emarginatus</i> 8.7	54	46				1			101
<i>Myotis capaccinii</i> 8.8	36					1			37
<i>Plecotus auritus</i> 9.3	375	228		5		5	3	1	618
<i>Myotis petax</i> 9.5						2			2
<i>Myotis annectans</i> 9.7		2							2
<i>Barbastella barbastellus</i> 9.7	50	418				8			476
<i>Plecotus</i> sp. 9.8	45						2	2	49
<i>Rhinopoma microphyllum</i> 10.0	3					7			10
<i>Pipistrellus nathusii</i> 10.2	133	22				2		1	158

Bat species and weight in grams	T.a.	S.a.	S.u.	A.o.	A.fl.	B.b.	A.fu.	A.n.	Total
<i>Myotis bechsteinii</i> 10.2	38	125		1		4			168
<i>Plecotus austriacus</i> 10.3	272	11		11					294
<i>Myotis daubentonii</i> 10.9	115	85	5	18			4		227
<i>Nycteris thebaica</i> 11.5	3								3
<i>Eptesicus nilssonii</i> 11.6	17	65	3		2	3	2		92
<i>Miniopterus schreibersii</i> 11.9	55	39				1		1	97
<i>Myotis</i> sp. 12.1	69	1		2	195	4			271
<i>Rhinolophus blasii</i> 12.5	3								3
<i>Rhinolophus euryale</i> 12.9	10	36				6			52
<i>Myotis dasycneme</i> 13.2	33	16							49
<i>Rhinolophus</i> sp. 14.6	2							1	3
<i>Rhinolophus bocharicus</i> 15.1								6	6
<i>Nyctalus leisleri</i> 16.0	24	7							31
<i>Vespertilio murinus</i> 16.6	119	1725			2	51		3	1900
<i>Vespertilio</i> sp. 16.8						1			1
<i>Vespertilio sinensis</i> 17.0				12					12
<i>Rhinolophus mehelyi</i> 17.6	2								2
<i>Eptesicus</i> sp. 18.5		1							1
<i>Hesperoptenus</i> sp. 18.8		1							1
<i>Otonycteris hemprichii</i> 19.0	56					16		5	77
<i>Eptesicus bottae</i> 20.5	19	13				1			33
<i>Myotis blythii</i> 21.3	199	75		1		41		1	317
<i>Eptesicus serotinus</i> 23.4	985	281		120		28		1	1415

Bat species and weight in grams	T.a.	S.a.	S.u.	A.o.	A.fl.	B.b.	A.fu.	A.n.	Total
<i>Rhinolophus ferrumequinum</i> 23.5	135	35				10			180
<i>Taphozous nudiventris</i> 28.0	37	2			2	3			44
<i>Nyctalus</i> sp. 28.1	1								1
<i>Nyctalus noctula</i> 28.3	425	1033		274		19		10	1761
<i>Myotis myotis</i> 32.8	1981	916	1	3		46		2	2949
<i>Tadarida teniotis</i> 38.0	9	3		1					13
<i>Nyctalus lasiopterus</i> 40.1	2	1							3
<i>Cynopterus sphinx</i> 46.0	1								1
<i>Scotophilus heathi</i> 50.0		1							1
<i>Rousettus leschenaulti</i> 60.0	1								1
<i>Rousettus aegyptiacus</i> 135.0	90					4			94
Chiroptera (unidentified)	191	121	1	114	11	54	3	21	515
Total	9356	8312	12	1510	220	346	22	86	19,864
Percentage of the total	47.1	41.9	0.1	7.6	1.1	1.7	0.1	0.4	100.0

T.a. = *Tyto alba*: [29–58], S.a. = *Strix aluco*: [7, 59–90]; S.u. = *Strix uralensis*: [61, 91–96]; A.o. = *Asio otus*: [38, 42, 43, 60, 61, 81, 92, 97–127]; A.fl. = *Asio flammeus*: [46, 92, 128–133]; B.b. = *Bubo bubo*: [37, 60, 61, 92, 134–154]; A.fu. = *Aegolius funereus*: [60, 61, 86, 155–161]; A.n. = *Athene noctua*: [45, 60, 61, 74, 103, 162–177].

Table 1.

Numerical occurrence of bat species in increasing order of weight and unidentified bats in the diet of the most studied owl species in Eurasia.

has taken bats with the average weight of only 8.9 g (**Table 3**). Bat sizes range from 5.1 g, species like *Pipistrellus pygmaeus*, to 135 g species like *Rousettus aegyptiacus* (**Figure 1**). In the diet of owls, an average of 18.5 species of bats was found: barn owl 40, tawny owl 33, eagle owl 27, long-eared owl 18 and little owl 15 (**Table 3**). The remaining three species, short-eared, Tengmalm's and Ural owls had only eaten five species, each.

The average and maximum percentages of bats that have been eaten by the most studied Eurasian owls are shown in **Table 2**. Bats comprise only a very small part of an owls' diet; their percentage share amongst all prey is usually much less than 0.2% (**Table 2**). The very low percentage of bats in the food of owls suggests that bats are normally not a profitable prey item for owls, quite possibly because of the time and energy needed to capture them.

Owl	Average % of bats	Sample size	Author(s) and area	Maximum % of bats	Sample size	Author(s) and area
Barn owl (<i>Tyto alba</i>)	0.12	4,023,465	Roulin and Christe [29] Europe	26.6	2931	Sommer et al. [178] Germany
Tawny owl (<i>Strix aluco</i>)	0.07	19,902	Mikkola [7] Europe	30.5	13,791	Obuch [59] Slovakia
Ural owl (<i>Strix uralensis</i>)	0.06	1739	Jäderholm [91] Finland	0.3	1983	Rosina and Shokhrin [92] Far East, Russia
Eagle owl (<i>Bubo bubo</i>)	0.08	29,277	Jánossy and Schmidt [134] Eurasia	5.9	763	Rosina and Shokhrin [92] Far East, Russia
Long-eared owl (<i>Asio otus</i>)	0.04	793,309	Birrer [179] Eurasia	29.3	3561	Tian et al. [97] Beijing, China
Short-eared owl (<i>Asio flammeus</i>)	0.04	5449	Mikkola [7] Europe	39.3	516	Djilali et al. [128] El Golea, Algeria
Tengmalm's owl (<i>Aegolius funereus</i>)	0.04	9698	Mikkola [7] Finland	0.2	581	Uttendörfer [60] Germany
Little owl (<i>Athene noctua</i>)	0.01	23,899	Schönn et al. [180] Europe	2.8	360	Barbu and Sorescu [162] Romania
Scops owl (<i>Otus scops</i>)	0.03	6871	Malle and Probst [181] Europe	0.1	2152	Muraoka [182] Austria

Table 2.
 Average and maximum numerical percentages of bats that have been eaten by European owls.

Owl species	Average weight of the owl	Number of bats in the diet	Number of bat species in the diet	Total weight of bats in the diet	Minimum weight of eaten bat species	Maximum weight of eaten bat species	Average weight of all bats eaten
<i>Aegolius funereus</i>	139.5	19	5	169.7	6.1	11.6	8.9
<i>Athene noctua</i>	166.0	65	15	897.3	5.5	32.8	13.8
<i>Asio otus</i>	310.3	1396	18	17,696.3	5.5	38.0	12.7
<i>Tyto alba</i>	332.5	9165	40	164,934.2	5.1	135.0	18.0
<i>Asio flammeus</i>	355.5	209	5	2525.7	5.5	28.0	12.1
<i>Strix aluco</i>	514.3	8191	33	125,874.7	5.5	50.0	15.4

Owl species	Average weight of the owl	Number of bats in the diet	Number of bat species in the diet	Total weight of bats in the diet	Minimum weight of eaten bat species	Maximum weight of eaten bat species	Average weight of all bats eaten
<i>Strix uralensis</i>	839,5	11	5	134.7	6.1	32.8	12.3
<i>Bubo bubo</i>	2542.5	292	27	6267.5	5.5	135.0	21.5
Total/ average		19,348	18.5	318,500.1	5.1	135.0	16.5

Table 3.

Numbers and weights of bats eaten by European owls in increasing order of weight. The correlation between owl weight and average bat prey weight is 0.736 which is significant at the level of $p < 0.05$. Weights shown are in g.

**Figure 1.**

An eagle owl has brought to its nest a female Egyptian fruit bat with a baby still sucking when figure was taken in 2008. Courtesy of Ezra Hadad, Israel.

Leading the level of bat consumption is the barn owl, although the absolute value, compared to other prey, is a very modest 0.12% (**Table 2**). No other owl species has taken bats over 0.1% in any large study samples. But the percentage rises markedly depending on the availability of bats as owls respond to increasing overall bat abundance in the environment [183]. Small maximum value samples show that near bat caves or in otherwise bat-rich biotopes, the prey share of bats can be significantly higher, up to 25–39% (**Table 2**).

4. Discussion

Contrary to other mammalian orders, bats face a very low risk of predation. Nocturnality and the capacity to reach remote shelters by active flight offer little opportunities for diurnal avian and terrestrial mammalian predators [21]. It has been shown that non-predator and non-accidental mortality of bats (probably caused by a disease, parasites or starvation) measured inside the fortifications

is higher during transitory periods preceding and following the period of deep hibernation, in which mortality is the lowest [184].

In the Far East, it has been noted that the eagle owl eats more bats during the autumn and close to the seashore where, most probably, it hunts these bats during their seasonal spring and autumn migrations along the coast [92].

Bats flying along line landscape elements (forest edges, shore and tree lines) or in open spaces are more exposed to predation [185].

Although the diet studies are equally numerous, in Europe the short-eared owl catches many fewer bats than the long-eared owl, likely due in part to its diurnal activity in open habitat (with fewer bats). However, in Algeria (North Africa), three short-eared owl pairs had more bats (39% by number and 9.3% by biomass) in their diet when long-eared owls in the same area preferred rodents and birds [128].

In the case of the long-eared owl, Garcia et al. [98] concluded that on a geographical scale, bat abundance does not seem to reflect bat availability for owls, maybe because hunting strategies for preferred prey such as small rodents are not well suited for the capture of flying bats. Bats occurred in many long-eared owl diets across the Mediterranean region, but their contribution remained largely irrelevant, although some bat aggregations were a locally important food source for some individual owls during certain periods.

Large barn owl diet samples show well how bats are eaten more in the south than in the north: In Britain, the frequency of bats was only 0.03% of 66,276 prey [185] and was 0.03% out of 102,588 prey in Belgium [30] but was 0.06% of 18,768 prey in the Pyrenees and 0.11% of 10,716 prey in Corsica [30].

Some cave samples for the tawny owl (30.5% bats out of 13,791 prey items) date back to the second half of the eighteenth century [61]. It is not known if the climate was more favourable to bats at that time, but they must have been more abundant. Roulin and Christe [29] have also shown that bat predation by barn owls has decreased during the last 150 years, due to historical declines in bat populations during the last century [186]. This decline could be caused by the human impacts which have affected many bat species. Lesiński [187] showed that in Poland, tawny owls ate fewer bats in the 1980s, possibly due to the intensive use of toxic pesticides during those years.

5. Conclusions

Owls prey on bats rarely and opportunistically, although bat aggregations could be a locally important food source for some species and individual owls during certain periods. Also, the decrease in the main prey (rodent) abundance can lead owls to expand their diet and include bats. It has been said that pellet studies could underestimate or even miss small bats taken by owls [185]. This study shows, however, that all sizes of bats are widely represented in the diet of the studied owls. That larger owls tend to take larger bat prey could be useful in archaeological cave studies when trying to identify the original predator of recovered bone/fossil remains [188].

We found two main obstacles in the food studies of European owls: first, several studies did not present complete lists of prey numbers or frequencies (often bats are combined with shrews, as insectivorous mammals), and second, identification skills to name the bat species showed a large variation (in this material we had 515 unidentified bats). We urge future owl diet studies to include complete prey lists to provide future reviewers with more accurate bat occurrence data.

Although the number of bats found in owl pellets can be small, such data collected may represent important faunistic and biodiversity contributions, particularly for rare species. Many bat species still have a 'data deficient' conservation label, and even in the most recent atlas of Bats in many European countries, the data on distribution of some bat species remains very scarce and incomplete [31].

Acknowledgements

We thank Dr. Risto Tornberg, University of Oulu, Finland, for helping with the statistics and David H. Johnson, Director of the Global Owl project, for the helpful editorial comments and input on the project. Jevgeni Shergalin kindly obtained and translated a few Russian books and papers for this study. We also thank Ezra Hadad for the kind use of his photograph.

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Owl Beliefs in Kyrgyzstan and Some Comparison with Kazakhstan, Mongolia and Turkmenistan

Heimo Mikkola

Abstract

So far the Central Asian owl beliefs have not been well studied. As I have had opportunities to live and visit some countries regularly since 2009, it became possible to study owl beliefs mainly in Kyrgyzstan but also comparing some findings with Kazakhstan, Mongolia and Turkmenistan. In Kyrgyzstan, 124 persons were interviewed in 2010: 82 males and 42 females. Age of respondents varied from 12 to over 60 and all lived in the capital area of the country. Half of the respondents listed owls as wise and 43% just as a bird, and nobody saw the owl as a bird bringing bad luck. On the contrary, 34% believed that owls are helpful and bring good luck. Kazakhstan shares a Central Asian veneration of owls. Eurasian eagle owl feathers are used as precious amulets protecting children and livestock from evil spirits. The main reason why so many Mongolian people hold the owl to be sacred could be the history that the owl once saved the life of Genghis Khan, king of kings and supreme Khan of all the Mongols and Kalmyks in Tartary Empire. For the Turkmens, the little owl is a sacred bird, killing of which would be a great sin.

Keywords: owl beliefs, Kyrgyzstan, Kazakhstan, Mongolia, Turkmenistan

1. Introduction

The entire area of the Kyrgyz Republic is 200,000 km² making it roughly five times the size of Switzerland. The highest mountains reach well over 7000 m (Lenin 7134 m and Pobeda 7439 m). Only 4.5% of the country is covered by forest and there are three large natural lakes. The Kyrgyz Republic does not have very rich birdlife, and most birds have large and inaccessible territories. Therefore, it is no wonder that there are hardly any bird-related organisations and very few bird-watchers. People are generally not very interested in birds and ignore them just as they do with many other things and items that do not belong to them. It seems that hunters are people who still go into the field. They make many observations, but the information is easily lost as it is not collected or stored. Hunting is not very common in the Kyrgyzstan, and it is generally restricted to quails, pheasants, partridges, ducks and pigeons. All other birds are protected including their nests. Luckily



Figure 1. Tawny owl (*Strix aluco*) is a red data bird in Kyrgyzstan. Photo: courtesy of Jeff Martin.

hunters are not normally killing nonhunting species understanding that especially species mentioned in the *Red Data Book* should not be hunted.

According to Van der Ven [1] some 400 different bird species have been seen in the Kyrgyz Republic, these including 10 owl species: common scops owl (*Otus scops*), pallid scops owl (*Otus brucei*), snowy owl (*Bubo scandiacus*), Eurasian eagle owl (*Bubo bubo*), tawny owl (*Strix aluco*), northern hawk owl (*Surnia ulula*), little owl (*Athene noctua*), Tengmalm's owl (*Aegolius funereus*), long-eared owl (*Asio otus*) and short-eared owl (*Asio flammeus*). Lately I have added one more owl, great grey owl (*Strix nebulosa*), into this list [2]. The *Red Data Book* of Kyrgyz Republic [3] includes two owl species: Eurasian eagle owl and tawny owl (**Figure 1**) in Status VII, Least Concern (LC).

2. Methods

By using the Global Owl Project interview form in Russian, 124 persons were interviewed in 2010: 82 males and 42 females. Age of respondents varied from 12 to over 60 and all lived in the capital area of the country. Rural areas could have given different results, but then it would have required the interview form in Kyrgyz or Uzbek languages. Russian language is widely spoken only in the urban areas.

3. Results

3.1 General owl knowledge

From the respondents 98% knew that owls are birds, but 2% were not sure. Around 89% had seen an owl, 7% have not and 4% were not sure; similarly, 73% have heard owls calling, 19% have not and the remaining 8% were not sure. Interestingly 77% were convinced that there are no owls in their living places, only 18% were sure that there are owls near the places where they live, and 5% were not sure. This could be a correct situation in the Bishkek city where I never saw an owl from my rented flats between 2009 and 2011.

3.2 Identification of owl species

Only female respondents (2) stated that they know more than six owl species, while only one male knew 3–5 species. Almost every third respondent were not able to identify any owl species: 29% of the females and 30% of the males. These percentages would indicate that there is no real difference in the owl species identification skills between females and males.

3.3 Biotopes

Almost all respondents knew that the owls live predominantly in the forest (97%). Other biotopes were listed as: mountains, 31%; grasslands, 25%; farms, 18%; cities, 10%; and elsewhere, 3%.

3.4 Food

Again, a great majority knew correctly that owls eat rodents and other small mammals (95%). Other food items got the following percentages: snakes, 31%; insects, 30%; lizards, 23%; frogs, 20%; fish, 18%; seeds, 16%; birds, 8%; fruits, 3%; and chicken, 2%. Nobody listed cats or dogs as the owl prey items.

3.5 Breeding

Nesting places of the owls were known as follows: tree holes (89%), other bird nests (20%), cliff ledges (12%), rooftops in the buildings (10%) and much less importantly nest boxes (3%) and burrows (2%).

3.6 Attitudes towards owls

Interestingly half of the respondents listed owls as wise, 43% just as a bird and 26% as creator beings. Nobody saw the owl as a bird bringing bad luck. On the contrary, 34% were convinced that owls are helpful and bring good luck. In addition, respondents gave the following answers: helpful for medicine, 10%; scary, 5%; powerful spirits, 2%; and 5% were not sure. Unfortunately, people did not explain further the medicinal value of the owls as that was not specifically asked during the interviews.

3.6.1 What is your attitude about protecting owls?

Despite very positive general attitudes, people were not so convinced that the owls should be protected. Only 62% felt that owls need protection, 15% would leave owls without protection, and 23% could not make up their mind in this matter.

3.7 Feelings about owls

3.7.1 How do you feel to talk about owls?

Eighty percent of the respondents stated that it is neutral/indifferent to talk about owls, none were frightened to do that, and 8% felt happy to talk about owls. The remaining 12% were not sure which feelings they had.

3.7.2 How do you feel when you hear an owl calling?

More than half of the respondents (56%) felt that it was neutral/indifferent to hear an owl calling, but 12% were frightened, and 13% were happy. Around 16% had never heard an owl calling, and 3% were not able to express their feelings.

3.7.3 How do you feel when you see an owl?

Again, over half (51%) felt neutral/indifferent seeing an owl, but 12% were frightened, and 17% were happy. Around 15% had never seen an owl, and 5% were not sure about their feelings.

3.7.4 How do you feel when someone tells you stories or legends related to owls?

Well over half (54%) feels neutral/indifferent, nobody feels frightened and 10% feels happy. Even 27% had never heard any legends or stories on owls, and 9% were not sure what they should answer.

3.8 Owl classifications

Owl classifications based on the 124 interviews in Kyrgyzstan.

Owls are	Female (%)	Male (%)	Total (%)
Harmless	0	3	2
Not important	3	1	2
Frightening	5	5	5
Important	21	24	22
Bad omen	3	1	2
Beneficial	65	65	65
Unsure to classify	3	1	2
Total	100	100	100
Number of interviews	42	82	124

The table above shows the owl classifications made by the male and female respondents. Interestingly male and female answers are very similar as 65% of both sexes classified owls as beneficial and 21–24% as important. Only one female and one male connected owl with bad omen, and 5% of females and males consider them frightening. One of both sexes was unsure to classify.

3.9 Additional cultural aspects of owls

3.9.1 Have you or do you know someone who has eaten owl meat?

Almost all respondents (95%) were sure that nobody eats owl meat in the Kyrgyz Republic, but 5% were not sure.



Figure 2.
*Eagle owl (*Bubo bubo*) feathers in talisman market. Photo: courtesy of Annegret and Michael Stubbe.*

3.9.2 Have you, or somebody you know, used owl eggs for some purpose?

One respondent answered yes, but without any further explanations. Another was not sure, but 98% were sure that nobody eats owl eggs in Kyrgyzstan.

3.9.3 Have you, or someone you know, used owl feathers, bones or meat?

As far as understood, all respondents were referring to the use of feathers only, not bones or meat. One third (32%) of both males and females knew people using the owl feathers (**Figure 2**) as talisman or head-dress. But well over half (63%) of the respondents did not know anybody using owl feathers, and 5% were not sure.

It is not known how often owls are killed to get the feathers, especially in the rural areas. Only one respondent had a friend who had killed an owl. This hunter made nicely banded bundles of the great grey owl breast feathers and sold those to his friends as talismans for the cars to protect drivers against traffic accidents. Large and soft owl feathers are used commonly to decorate traditional folk costumes and head-dress. Interestingly the *Red Data Book* [3] recommends breeding eagle owls in captivity in order to get moulted feathers from live birds without killing them. Many families in the country have a long tradition in keeping eagles and hunting falcons at home, so they would know well how to take care of large owls as well.

During my stay in the country between 2009 and 2011, I don't recall seeing any owl figurines for sale in the market places, but even the National Museum has an example of an eagle owl feather talisman, and some NGOs have printed owl calendars which are often seen in the walls of the government offices.

This may be the first time when owl beliefs have been investigated through an interview study in Central Asia. Owls are not feared but rather ignored.

4. Kazakhstan

Van Orden and Paklina [4, 5] have described how, characteristic to the region (cf. Kyrgyzstan and Mongolia), owl feathers are used in abundance for decoration. Typically, tufts of feathers from eagle owls are placed in strategic places such as



Figure 3.
*Little girl with beautifully adorned hat (including eagle owl feathers), Baiga festival, eastern Kazakhstan.
Photo: courtesy of Van Orden and Paklina.*



Figure 4.
A young lady with eagle owl protection in her hat. Photo: courtesy of Van Orden and Paklina.



Figure 5.
Small boy with cap adorned with eagle owl feathers during a circumcision ritual in eastern Kazakhstan. Photo: courtesy of Van Orden and Paklina.



Figure 6.
A pretty lady with complicated hat decorated with eagle owl feathers to protect her with sacred powers during the festivals and ceremonial gatherings. Photo: courtesy of Van Orden and Paklina.

bedrooms and cradles or used as amulets. Hats worn as part of celebrations or festive gatherings are also decorated with tufts, usually taken from the birds' breast or mantle. In local tradition the feathers are thought to be reincarnations of guardian spirits and endowed with sacred powers (see **Figures 3–6**).

The use of feathers is described as massive in scale and has, not surprisingly, resulted in the eradication of eagle owls in large parts of Kazakhstan [5].

However, in recent years local tribes have taken to explore what are described as “antiquated” power lines where large numbers of owls and other birds of prey are being electrocuted providing easy access to feathers for ornamental purposes.

In the village of Orlovka, in the east of the country, the authors saw a collection of 14 steppe eagles (*Aquila nipalensis*), 4 eastern imperial eagles (*Aquila heliaca*), 3 golden eagles (*Aquila chrysaetos*), 6 steppe buzzards (*Buteo b. vulpinus*), 5 upland buzzards (*Buteo hemilasius*), 2 saker falcons (*Falco cherrug*) and 4 eagle owls. The village chief told that all these birds had been found beneath power lines between Orlovka and Ust-Kamenogorsk [5].

This again appears to be only the “tip of the iceberg” given that similar power lines are still in use all over southern Central Asia.

Electrocuted birds are currently thought to be the main source of feathers used in traditional wears and amulets as the wildlife protection and conservation concerns are well understood in the modern Kazakhstan [5].

5. Mongolia

In Mongolia, as in many parts of Asia, the owl is considered a protector and a divine ancestor, who helps to ward off evil spirits, famine and pestilence. One reason why so many eastern people hold the owl to be sacred could be the history that the owl once saved the life of Genghis Khan in the thirteenth century. He was king of kings and supreme Khan of all the Mongols and Kalmyks in Tartary Empire. It is interesting how differently this famous story can be told:

1. Sir John Mandeville, who in the fourteenth century travelled to the court of Genghis Khan in central Asia, also recounted how the Great Khan was saved by an owl: as he and his small army were fleeing from their enemies, his horse was killed, and he hid under a bush; an owl, alighting upon it, convinced his pursuers that nobody would seek refuge where the dreaded owl perched [6].
2. The warrior Khan had on this occasion been defeated by the enemy and was fleeing the battlefield with a small band of trusty followers. At one point he found shelter under a tree; and on a branch of this tree was perched an owl. His pursuers caught up with him but did not pause to investigate, because they did not believe that anyone could be so foolish as to hide beneath a tree on which such an unlucky bird was sitting. On they rode to continue their search elsewhere, and in this way, Genghis Khan was saved from certain death by the providential intervention of an owl [7].
3. Genghis Khan, the twelfth-century Mongol warrior, was once fleeing from a band of enemies, but was outnumbered and needed a place to hide. Eventually, he found a thick copse of trees, where he and his men sat silently. Very soon, an owl appeared and sat on a tree at the edge of the wood. When the opposing forces saw the bird, they knew that Genghis and his men couldn't be there if the owl sat so peacefully. They therefore moved away, and the Mongols escaped. Genghis Khan then adopted the owl as a good luck charm—from then



Figure 7.
Talisman market in Bajan-Ölgij, Western Mongolia. Photo: courtesy of Annegret and Michael Stubbe.



Figure 8.
Owl feather talismans in the market in Bajan-Ölgij, Western Mongolia. Photo: courtesy of Annegret and Michael Stubbe.

on, he and his followers wore owl feathers and charms both to protect themselves from danger and pay tribute to their special saviour [8].

Annegret and Michael Stubbe kindly sent photos (**Figures 2, 7 and 8**) from the market in Bajan-Ölgij, Western Mongolia (the capital of the Kazakhian Almag). One can see eagle owl wings, legs and feathers in these photos which will be used for owl talisman (cf. also Kazakhstan and Kyrgyzstan). The feathers of eagle owls and also great grey and long-eared owls are thought to be reincarnations of guardian spirits with sacred powers.

6. Turkmenistan


Central Asian owl beliefs are still not well studied although I have had opportunities to live and visit some countries regularly since 2009, though mainly Kyrgyzstan and Kazakhstan. Neighbouring Turkmenians have an interesting belief on little owl *Athene noctua*. The local name in Turkmenistan is “bai gush” (rich bird), and it is a sacred species. To kill this owl is a great sin [9]. Hopefully this belief is valid also in the wider area of Central Asia.

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Edited by Heimo Mikkola

Owls are soft-plumaged, short-tailed, big-headed birds that have the most frontally situated eyes of all birds and they can blink the upper eyelids. This, together with a broad facial disc, gives owls all the right characteristics to make them attractive in our eyes. At the same time, some people fear their presence and even their calls, and there are more myths and beliefs about owls than there are about any other bird. Bats are often similarly feared as owls, partly because both of them inhabit the night; a place that is unknown and alien to us. Owls and bats symbolise all that is mysterious about the night and their complete mastery of the darkness only highlights our own deficiencies. In this book, we will get to know the relationships between bats and owls. This book describes the biological control of rats by owls in Malaysia, the prey-predator interactions in a tropical forest in Mexico, and provides an overview of the breeding biology of owls. From numerous owl belief and myth studies, described in this book are those of the lesser known Central Asian countries where owls are often worshipped for their supernatural powers.

Published in London, UK

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