



1 Introduction

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2 BARN OWLS



Barn owl flying to new horizons.

1.1 WHY IS THE BARN OWL SO INTERESTING?

A step above the others

The barn owl is popular because of its cosmopolitan distribution and close association with humans. Owls have fascinated us throughout history and across many cultures. Venerated or considered as bad omens, owls feature often in myths and legends. The barn owl is a fantastic organism for investigating physiology, reproductive biology, social interactions between family members and the causes and consequences of colour variation. More to come!

Barn owls fascinate not only the lay public but also scientists. This bird has traditionally been used to study the diet of avian predators and to teach ecology. Barn owl pellets contain extraordinarily well-preserved bones and cuticles of their prey. Among the 3696 papers reviewed for the present book, almost half (1630) were about diet analyses. But interest in the barn owl extends to many other areas as well. Compared to that of other species, the barn owl's variation in morphology, physiology and behaviour is quite remarkable. Some of the barn owl's physiological traits, such as its hearing capacity, are extremely efficient, while other traits, such as resistance to cold, are poorly developed.

The barn owl can therefore be considered a model organism for identifying general rules that govern the evolution of biodiversity. My aim in this book is to highlight the unique characteristics of this bird in an attempt to depict general biological phenomena. These characteristics include seven key traits.

Cosmopolitan Barn owls are found almost everywhere except in cold temperate and arctic regions. Only approximately twenty vertebrate species, including humans, are cosmopolitan. Studying barn owls can therefore help us understand the factors allowing some animals to thrive worldwide.

Physiology The barn owl is often used to study hearing capacity and the ability to fly silently. Its nocturnal habits and high reproductive rate have exerted strong selective pressure to evolve the ability to hunt very efficiently, necessitating the ability to detect prey by ear at great distances while flying stealthily. These abilities are of great interest to neurologists and to the aeronautical industry.

Reproductive potential Compared with other raptors, barn owls are prolific breeders. Annually they may produce up to three broods, with some containing up to twelve young. In places where conditions are favourable, they can breed throughout the year. This potential for reproduction enables an investigation into the evolutionary causes and consequences of such high reproductive rates. A large body of data can be collected from a great many descendants, which is unusual for a species of this size.

Hatching asynchrony The first nestling can be up to one month older than its youngest sibling. This is because the parents usually stagger the timing of the hatchings, which has the effect of generating less competition among the young for parental attention. Although hatching asynchrony is traditionally considered a way for parents to reduce brood size, a plethora of hypotheses have been presented to explain its adaptive function. Because the degree of hatching asynchrony in the barn owl is one of the most pronounced among birds, this species is a prime candidate for studying the causes and consequences of size differences between young siblings.

Peaceful sib–sib interactions Young siblings vocally negotiate priority of access to food resources, and nestlings feed and preen their siblings. Social interactions within barn owl nests are intricate: this provides insight into parent–offspring conflict and sibling competition and cooperation. Although, in any species, siblings are genetically related, observations and theory have predicted that family interactions tend to be conflictual rather than harmonious. The finding that young barn owls peacefully share resources suggests that sibling cooperation can also evolve.

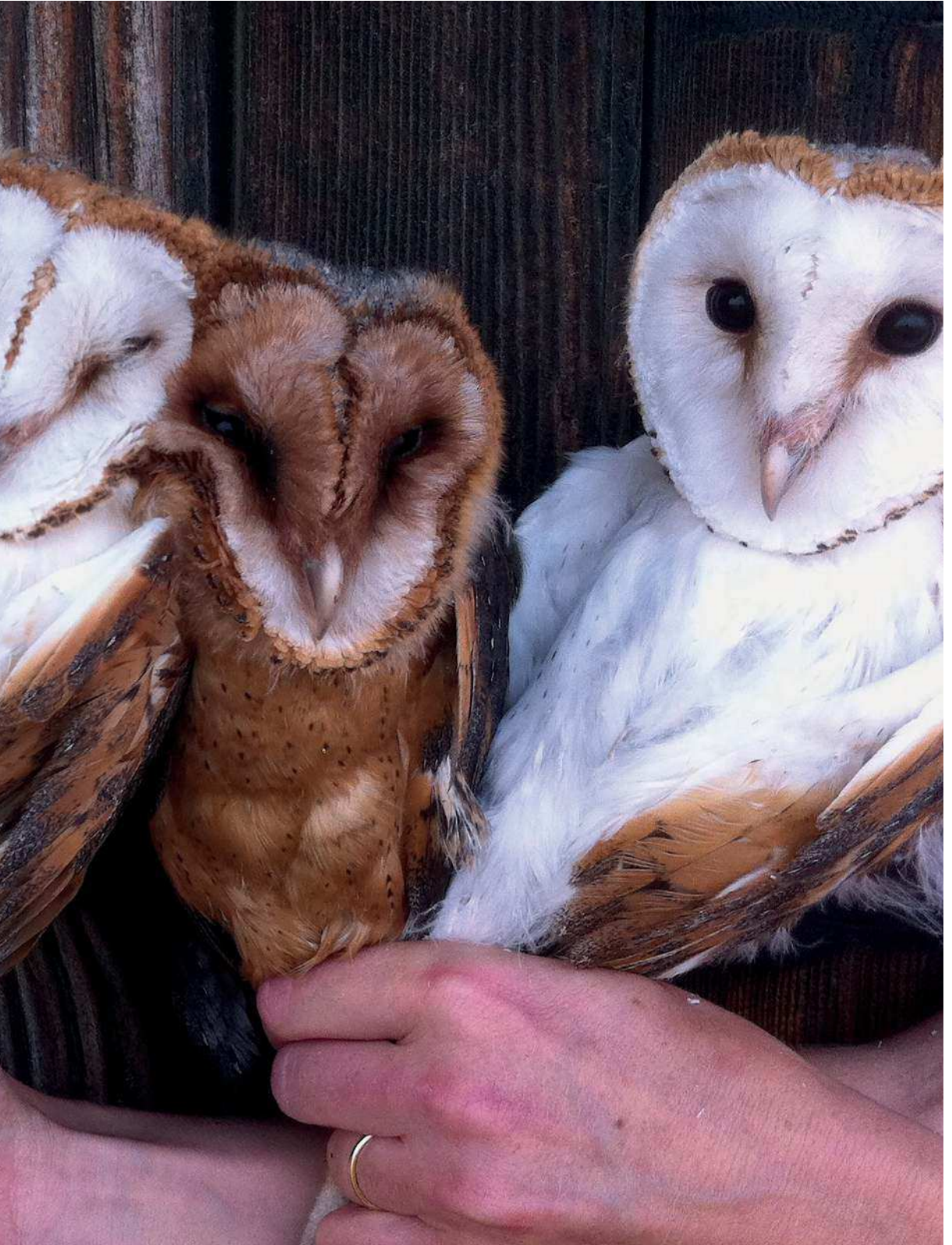
Plumage No two barn owls are alike. Some are dark reddish, some are white, and others are speckled with many large black feather spots. This variation is observed between and within populations and even between siblings. Melanin is the most common pigment in animals, and it has multiple functions. It confers camouflage, protects the skin and feathers from biophysical degradation and ultraviolet light, participates in thermoregulation, and signals aspects of quality to potential mates and conspecifics. The study of melanin-based colouration has become a major focus in evolutionary ecology, and to this end, the barn owl is a prime model system. In this species, differently coloured individuals adopt alternative reproductive strategies and behaviours.

Population dynamics Annual variations in population size are pronounced in the barn owl. Studying the processes underlying variation in population size requires species that are particularly sensitive to environmental factors, such as inclement weather and variation in food supply. Compared to those of other raptors, such as the kestrel, which exploits similar reproductive and foraging habitats, barn owl population sizes vary to a much higher degree. This difference raises a number of questions about why this species is one of the first to suffer under ecological deterioration and how individuals compensate once conditions improve by reproducing at a high rate. Because the barn owl is cosmopolitan and often lives close to humans, this species is suitable for monitoring the impact of human activities on wildlife and habitat degradation worldwide.

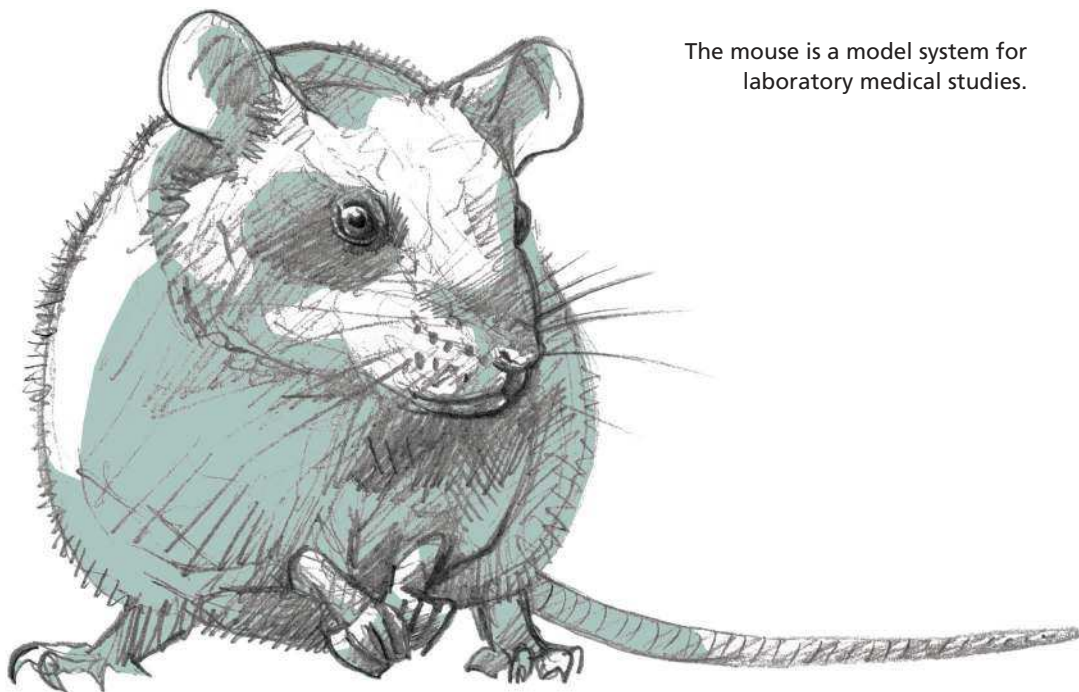
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Four barn owl siblings showing extreme variation in plumage colouration. © Alexandre Roulin



6 BARN OWLS



The mouse is a model system for laboratory medical studies.

1.2 WHY STUDY BARN OWLS INSTEAD OF LABORATORY MICE?

An emerging model system

The barn owl is beautiful, emblematic and scientifically interesting. Bird lovers agree that this bird should be studied in depth and protected, but why should funding agencies finance studies using the barn owl rather than biomedical or molecular studies using laboratory mice?

In science, fields such as genetics, immunology and cell biology make significant advances using mice, flies and rock cress. These model organisms are so well studied and easy to work with that the study of any other organisms can appear counterproductive to high-profile researchers. Science, biomedicine in particular, invests most of its human and financial resources in research based on model organisms; thus research on other species requires justification. Although model organisms have indeed provided invaluable scientific insights, their study also results in substantial limitations to obtaining a general understanding of nature.

Organisms evolve through natural selection, which ultimately modifies the frequency of genes present in the ancestral population. It is therefore necessary to consider the evolutionary history of each species to understand why a given adaptation initially evolved. For instance, owls living on an island may display a whitish plumage not because it confers camouflage but because the owls that initially colonized this island happened to be light rather than dark. Evolutionary ecologists, however, are mainly interested in understanding whether physiological, morphological and behavioural adaptations have evolved to address specific ecological factors. Therefore, evolutionary ecologists prefer to study organisms in their natural environment rather than in the laboratory.

My aim here is not to discredit laboratory studies in animal models but to explain why studying another species, such as the barn owl, in its natural habitat is complementary. To this end, I contrast laboratory and field studies using four arguments.

Artefact Animals living outside their natural environment may behave in strange ways. Furthermore, the adaptive function of specific traits may not be obvious when they are studied under laboratory conditions. Only studies of animals in their natural environment, such as studies on wild barn owls, can ultimately reveal the context under which adaptations have evolved.

Laboratory animals are not representative of wild counterparts Laboratory animals cope well with the stress induced by laboratory conditions, have a short generation time, and are prolific. Because all laboratory animals share these properties, scientific results based on studies using these animals may not necessarily be of general applicability, but rather are restricted to animals that are living under stressful laboratory conditions.

Artificial selection Animals bred for many generations evolve new behavioural, physiological and morphological traits adapted to laboratory rather than natural conditions. Conversely, barn owls have evolved in the wild, interacting with their biophysical environment and other wild animals. Studies of this bird can therefore provide important ecological insights with general applicability.

Biodiversity Nature finds many ways to solve a single problem. Science will repeatedly rediscover the same set of solutions if using the same set of organisms. Working with organisms other than those usually studied by most researchers will be refreshing, and will offer novel insight into old problems. Deciphering the complexity of ecosystems, and understanding life in its full diversity, therefore necessitates studying a variety of species in addition to those used in the laboratory.



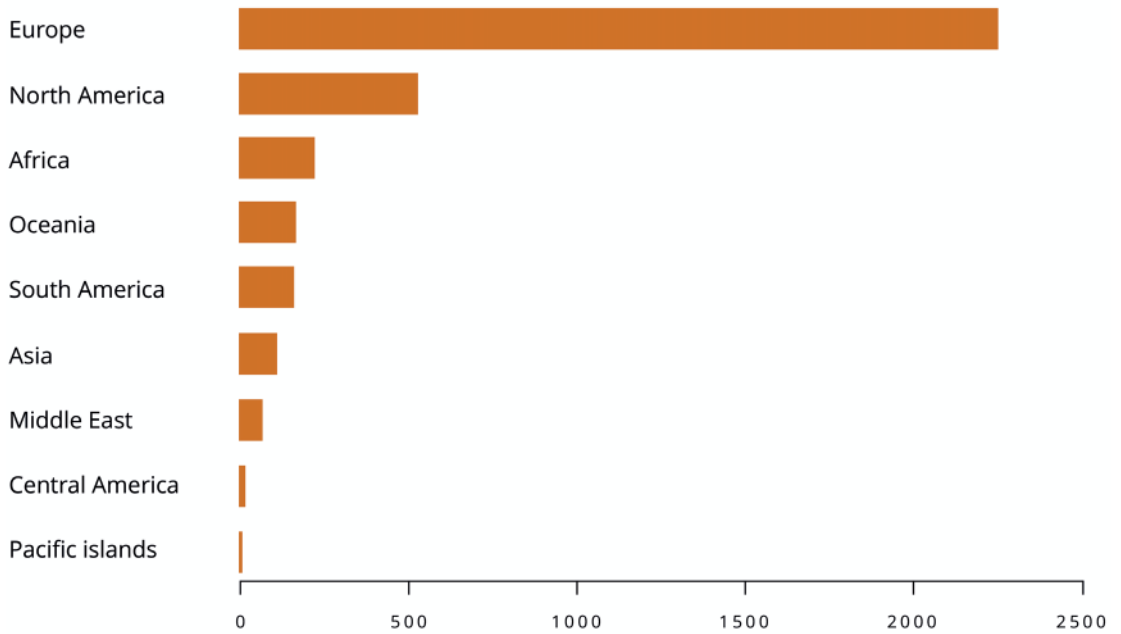
Thousands of papers and numerous books have been written on the barn owl. Library at the Swiss Ornithological Institute in Sempach. © Alexandre Roulin

1.3 THE RAW DATA

The barn owl gets a lot of attention!

This book is based on scientific literature published between 1853 and 2018 on the barn owl and its relatives. I searched for all papers published in international and local journals. This necessitated visiting libraries, contacting authors directly and searching the web. I explicitly searched for papers about the ecological and evolutionary aspects of barn owls, with no geographical restriction.

While I researched 3696 papers and books on the Tytonidae family (many of them not available in the *Web of Science*), there are still at least 650 published papers left to be referenced! The graph opposite illustrates the number of papers published about Tytonidae studied in different parts of the world. Approximately 61% of studies of barn owls have focused on the European population of western barn owls, with most studies stemming from fieldwork conducted in Germany (564 papers, 15.3%), followed by studies of the American barn owl (492 papers, 13.3%). Therefore, the greater availability of information on European or American barn owls is likely the result of a greater research effort in Europe and the USA than in Africa, the Middle East, Asia, Oceania, the Pacific islands, Central America and South America. My hope is that this book will stimulate further research worldwide.



Number of scientific papers on Tytonidae species from different areas of the world.

Some *Tyto* taxa are more studied than others, implying that the information reported in the present book is biased towards these taxa. For this reason, this book mainly draws on research carried out on the common barn owl (traditionally referred to as *Tyto alba*) unless otherwise stated. The term Tytonidae refers to all species of the genera *Tyto* and *Phodilus*.



A barn owl in an old temple in India. An iconic view of how close the barn owl is to humans.

1.4 EVOLUTION OF THE TYTONIDAE

The world is yours

The family Tytonidae most likely first appeared in Australasia. This family has successfully colonized all continents except Antarctica. Australasia contains the most diverse populations of Tytonidae.

Owls are the sister group to a diverse land-bird clade including mousebirds, trogons, cuckoo roller, coraciiforms and piciforms. Interestingly, all these land birds evolved from predators. Tytonidae diverged from typical owls (Strigidae) approximately 45 million years ago. At least thirteen Tytonidae taxa are extinct, and some were even larger than the imposing Eurasian eagle owl. For instance, the humerus of the extinct *Tyto gigantea* found in Italy measured 185 mm, compared to 73–85 mm in the contemporary Italian barn owl (*Tyto alba*).

Tytonidae evolution and world colonization The available genetic data indicate that the ancestors shared by Strigidae and Tytonidae probably existed around the middle Eocene (about