

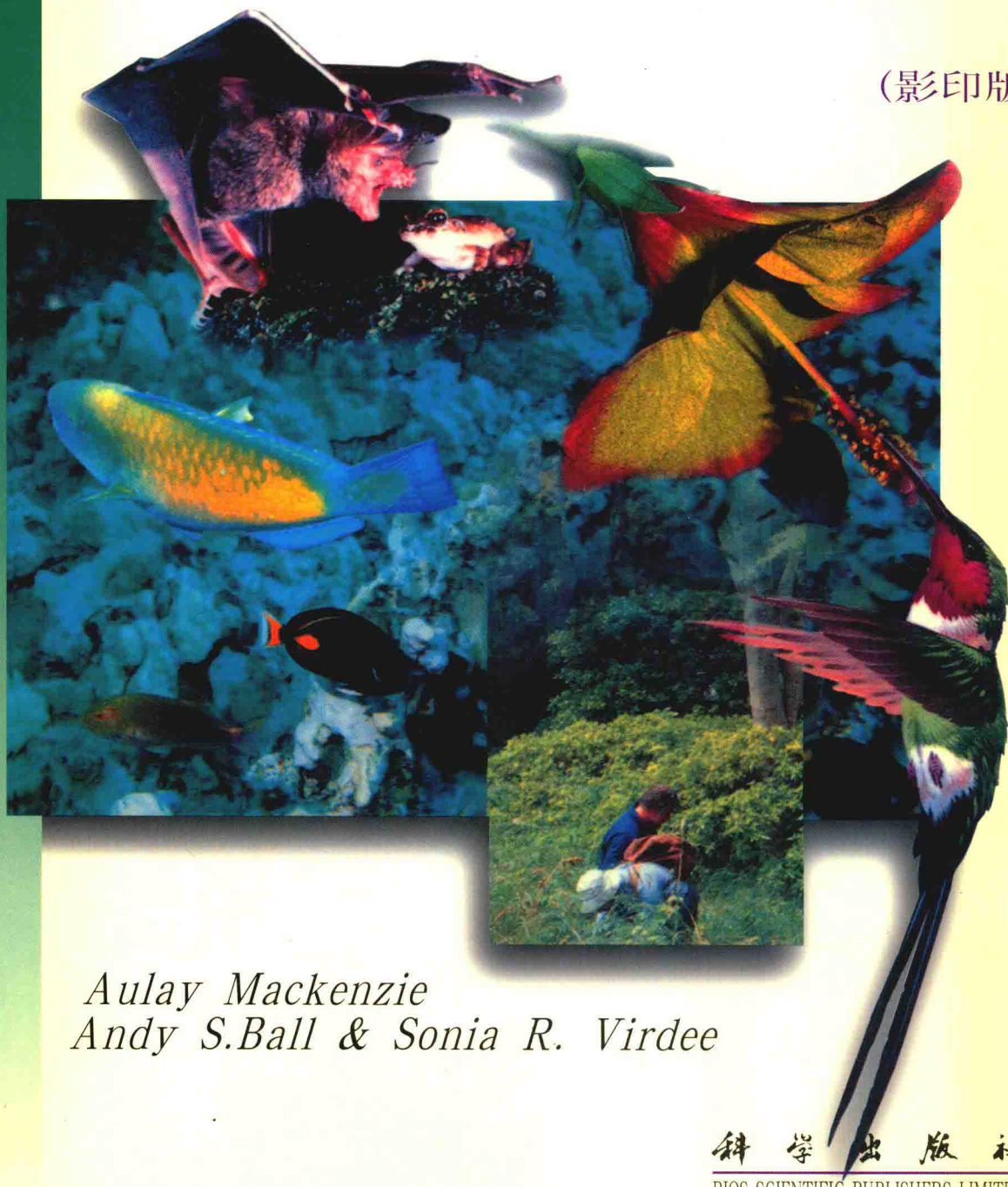
现代生物学精要速览

Instant Notes in

E C O L O G Y

生态学

(影印版)



*Aulay Mackenzie
Andy S. Ball & Sonia R. Virdee*

科学出版社

BIOS SCIENTIFIC PUBLISHERS LIMITED

现代生物学精要速览

Instant Notes in

ECOLOGY

生态学

(影印版)

A. Mackenzie

Department of Biological Sciences,
University of Essex, Colchester, UK

A.S. Ball

Department of Biological Sciences,
University of Essex, Colchester, UK



S.R. Virdee

University College Suffolk, Ipswich, UK



科学出版社



BIOS SCIENTIFIC PUBLISHERS LIMITED

1999

内 容 简 介

本套丛书是国外优秀教材畅销榜的上榜教材,面向大学生,由英国著名大学具丰富教学经验的一流教授编写。它以一种风格独特的描述方式,全面、系统地概括了学科的核心内容和前沿动态,并以一种便于学习、利于复习的形式,使学生能快速、准确地掌握知识,很好地指导学习和考试。书中英文使用最为自然、易懂的语句,是提高专业外语的最佳套书。本书是该系列中的生态学分册,共约 16 个章节。

A. Mackenzie, A. S. Ball and S. R. Virdee

Instant Notes in Ecology

Original edition published in the United Kingdom under the title of Instant Notes in Ecology

© BIOS Scientific Publishers Limited, 1998

图字:01-99-0188

科学出版社出版

北京东黄城根北街16号

邮政编码:100717

中国科学院印刷厂印刷

新华书店北京发行所发行 各地新华书店经售

*

1999年3月第一版 开本:787×1092 1/16
1999年9月第二次印刷 印张:21
印数:3 001—6 000 字数:476 000

ISBN 7-03-007304-5/Q·846

定价:43.00元

(如有印装质量问题,我社负责调换〈北燕〉)

Q-0846-12

现代生物学精要速览(Instant Notes)系列

Instant Notes in Biochemistry 《生物化学》

Instant Notes in Genetics 《遗传学》

Instant Notes in Molecular Biology 《分子生物学》

Instant Notes in Microbiology 《微生物学》

Instant Notes in Animal Biology 《动物生物学》

Instant Notes in Ecology 《生态学》

Instant Notes in Immunology 《免疫学》

Instant Notes in Neuroscience 《神经科学》

Instant Notes in Chemistry for Biologists 《生物学中的化学》

CONTENTS

Abbreviations	ix
Preface	x
Section A – Introduction to ecology	1
A1 What is ecology?	1
A2 Ten rules in ecology	3
Section B – Adaptation to the environment	11
B1 Adaptation	11
B2 Coping with environmental variation	14
B3 The niche	18
Section C – Climate	21
C1 Solar radiation and climate	21
C2 Microclimate	27
Section D – Water	31
D1 The properties of water	31
D2 Plants and water	34
D3 Animals and water	39
Section E – Temperature	43
E1 Temperature and metabolism	43
E2 Responses to temperature	47
E3 Temperature and species distribution	50
Section F – Radiation	53
F1 Solar radiation and plants	53
Section G – Nutrients	59
G1 Sources and cycles	59
G2 Plants and consumers	65
G3 Soil formation, properties and classification	67
Section H – Population ecology	71
H1 Populations and population structure	71
H2 Natality, mortality and population growth	75
H3 Density and density dependence	84
H4 Population dynamics – fluctuations, cycles and chaos	89
Section I – Competition	93
I1 The nature of competition	93
I2 Intraspecific competition	99
I3 Resource partitioning	102
Section J – Predation	107
J1 The nature of predation	107
J2 Predator behavior and prey response	111
Section K – Parasitism	117
K1 The nature of parasitism	117
K2 The dynamics of parasitism	122

Section L – Mutualism	129
L1 Mutualism	129
Section M – Life history patterns	135
M1 Life history	135
Section N – Behavioral ecology	145
N1 Social groups, cooperation and altruism	145
N2 Sex in ecology	149
Section O – Population genetics	157
O1 Genetic variation	157
O2 Speciation	163
Section P – Ecosystem processes	169
P1 Components and processes	169
P2 Primary and secondary production	174
P3 Food chains	179
Section Q – Communities	183
Q1 The community, structure and stability	183
Q2 Island communities and colonization	189
Q3 Community patterns, competition and predation	194
Section R – Community dynamics	201
R1 Succession	201
R2 Community responses to disturbance	208
Section S – Biomes	213
S1 Ecosystem patterns	213
S2 Grasslands	218
S3 Tundra	222
S4 Forests	224
S5 Deserts, semi-deserts and shrubland	228
S6 Saltwater biomes	231
S7 Freshwater biomes	236
Section T – Harvesting	241
T1 Harvesting theory	241
T2 Fishing and whaling	246
Section U – Pest control	251
U1 The pest problem and control strategies	251
U2 Pesticides and problems	255
U3 Biological control and integrated pest management	261
Section V – Conservation	265
V1 Rare species, habitat loss and extinction	265
V2 Conservation strategies	271
V3 Biological resources and gene banks	276
Section W – Pollution and global warming	283
W1 Air, water and soil pollutants	283
W2 Greenhouse gases and global warming	288
W3 Ozone	291

Section X – The ecology of agriculture	295
X1 Soil erosion and agriculture	295
X2 Nutrient, water and energy use	298
Further reading	305
Index	315

ABBREVIATIONS

ADH	alcohol dehydrogenase	IPM	integrated pest management
AE	assimilation efficiency	MEY	maximum economic yield
AIL	aesthetic injury level	MSY	maximum sustainable yield
BOD	biochemical oxygen demand	MVP	minimum viable population
CAM	crassulacean acid metabolism	NPP	net primary productivity
CAT	control action threshold	NVC	National Vegetation Classification
CE	consumption efficiency	PAR	photosynthetically active radiation
DBH	diameter at breast height	PCB	polychlorinated biphenyls
DDD	2,2-bis(<i>p</i> -chlorophenyl)- 1,1-dichloroethane	PE	production efficiency
DDT	dichlorodiphenyltrichloroethane	PVA	population viability analysis
EIL	economic injury level	RDZ	resource depletion zone
GPP	gross primary productivity	SMRS	specific mate recognition system
ICTZ	intertropical convergence zone	SOM	soil organic matter

PREFACE

The last 40 years have witnessed a vast expansion of both interest and knowledge in ecology. There has been a widening public awareness of the importance of ecological interactions, with particular focus on such issues as the impact of pesticides upon food chains and the loss of global biodiversity owing to habitat destruction. In parallel, a wide suite of advances in ecological understanding have been fuelled by progress in a number of other fields, notably molecular biology.

This great expansion in understanding has lead to a problem for the student of the subject, as leading textbooks have grown greatly in size and complexity to accommodate new theories and new data. Further, ecology courses are now an integral component of a wide range of biological science degrees. This book attempts to distil the key areas of ecology in a way which will help both full-time students of the subject and those studying ecology as a subsidiary subject.

Instant Notes in Ecology is designed to give students rapid, easy access to key ecological material in a format which facilitates learning and revision. The book is divided into 62 topics which cover material at the level we would expect of good first/second year students. Each topic starts with a short list of 'Key Notes' — a revision checklist — before explaining the subject matter. Further reading is included at the end of the book for students who wish to delve more deeply into selected areas of interest.

Section A provides a brief outline of the area of ecology, and includes a list of 'rules' in ecology which derives from some common mistakes and pitfalls that the authors' experiences suggest many students are liable to make. Sections B to G cover the key aspects of the abiotic environment which affect organisms (climate, water, temperature, radiation, nutrients) and how organisms are adapted to their environment. Populations and interactions are covered in Sections H to O, including population ecology, competition, predation, parasitism, mutualism, life histories, behavioral ecology and population genetics. In Sections P to S, ecosystems, biomes and community patterns and processes are dealt with. In the final five Sections, T to X, some key issues in applied ecology are dealt with, including harvesting (with a focus on fisheries), conservation, pollution and global warming and agriculture.

How should you use this book as a student? Your course will almost certainly differ in structure from the layout here. However, the breakdown of the text into small manageable topics, each cross-referenced, will allow you to easily navigate your way to the information you seek.

Thanks are due to those we were not with while writing this book: Ishbel, Eilidh, Sara, Simon and Katrina. We also thank Rachel Offord, Lisa Mansell and Fran Kingston at BIOS for fortitude in the face of evasion.

Aulay Mackenzie, Andy Ball and Sonia Virdee

A1 WHAT IS ECOLOGY?

Key Notes

A definition of ecology

Ecology is the study of the interactions between organisms and their environment. The 'environment' is a combination of the physical environment (temperature, water availability, etc.) and any influences on an organism exerted by other organisms – the biotic environment.

Individuals, populations, communities and ecosystems

There are four identifiable subdivisions of scale which ecologists investigate: (i) considering the response of individuals to their environments; (ii) examining the response of populations of a single species to the environment, and considering processes such as abundance and fluctuations; (iii) the composition and structure of communities (the populations occurring in a defined area); (iv) the processes occurring within ecosystems (the combination of a community and the abiotic components of the environment), such as energy flow, food webs and the cycling of nutrients.

A definition of ecology

Ecology is the study of the interactions between organisms and their environment. There are two distinct components to the 'environment': the **physical environment** (comprising such things as temperature, water availability, wind speed, soil acidity) and **biotic environment**, which comprises any influences on an organism that are exerted by other organisms, including competition, predation, parasitism and cooperation.

Within ecology there are a number of fields, either focusing on specific areas of interest or using particular approaches to address ecological problems. For example, **behavioral ecology** is concerned with explaining the patterns of behavior in animals. **Physiological ecology** explores the physiology of an individual and considers the consequences on function and behavior. A particular emphasis on the impact of evolution on current patterns is the focus of **evolutionary ecology**. A recent development has been the use of molecular biology to directly tackle ecological problems – **molecular ecology**. The domains of **population ecology** and **community ecology** are described below.

Ecological studies are not restricted to 'natural' systems – understanding both the human effects on nature and the ecology of artificial environments (such as crop fields) are important areas of study.

Individuals, populations, communities and ecosystems

Ecology can be considered on a wide scale, moving from an individual molecule to the entire global ecosystem. However, four identifiable subdivisions of scale are of particular interest, (i) **individuals**, (ii) **populations**, (iii) **communities** and (iv) **ecosystems**.

At each scale the subjects of interest to ecologists change. At the individual level the response of **individuals** to their environment (biotic and abiotic) is the key issue, whilst at the level of **populations** of a single species, the determinants of abundance and population fluctuations dominate. **Communities** are

the mixture of populations of different species found in a defined area. Ecologists are interested in the processes determining their composition and structure. **Ecosystems** comprise the biotic community in conjunction with the associated complex of physical factors that characterize the physical environment. Issues of interest at this level include energy flow, food webs and the cycling of nutrients.

It should be noted that the terms 'population', 'communities' and 'ecosystems' are often ill-defined. It is often not possible to clearly delineate where one population stops and another starts, and the same problem occurs with communities and ecosystems. To some degree, these terms simply represent convenient simplifications by which we can categorize the natural world.

A2 TEN RULES IN ECOLOGY

Key Notes

What are these rules?

The authors' experience of teaching ecology has given them experience of some common pitfalls which ecology students often make. This list, designed to counter these pitfalls, is neither comprehensive nor mutually exclusive, but we hope will nevertheless serve as a useful guide to protocol.

Rule 1

Ecology is a science.

Ecology is a purely scientific discipline which aims to understand the relationships between organisms and their wider environment. It is important to segregate political and social impacts of ecological understanding from the scientific viewpoint.

Rule 2

Ecology is only understandable in the light of evolution.

The huge diversity of organisms, and the wealth of variety in their morphologies, physiologies and behavior are all the result of many millions of years of evolution. This evolutionary history has left an indelible impression on each and every individual. It is only possible to make sense of the patterns we find today in the light of this evolutionary legacy.

Rule 3

Nothing happens 'for the good of the species'.

A very common misconception is the idea that patterns of behavior in organisms which appear to be costly to an individual occur 'for the good of the species'. This is absolutely and completely wrong. Natural selection will favor those genes which are passed on to the most offspring, even if these genes may cause a reduction in the species' population size.

Rule 4

Genes and environment are both important.

The environment an organism finds itself in plays an important role in determining the options open to that individual. The genes which define an organism's makeup are also of fundamental importance. To understand ecology it is important to appreciate the fundamental nature of both of these factors and the fact that they interact.

Rule 5

Understanding complexity requires models.

Ecology is a complex subject, with huge variation at almost every scale – millions of species, each with considerable genetic variation, varying numbers and ever-changing behaviors in a complex and dynamic environment. To understand it, it is necessary to clearly identify specific questions and then formulate hypotheses which can be tested. It is often very useful to frame the hypothesis in mathematical terms to avoid ambiguity and confusion which are often inevitable in a verbal model. Mathematical models are widely used in ecology.

Rule 6**'Story-telling' is dangerous.**

In attempting to explain ecological patterns or relationships, it is easy to slip into a make-believe world where every observation is readily explained by some *ad hoc* assertion – 'story-telling'. The temptation to advance hypotheses as facts should be avoided at all costs.

Rule 7**There are hierarchies of explanations.**

For any observation there is often an immediate cause that can be diagnosed. Often this causal explanation is insufficiently informative and we need to probe deeper to reach a fuller grasp of the situation. Even if a phenomenon is 'explained' there may well be further and deeper explanations which allow us to see the fuller picture.

Rule 8**There are multiple constraints on organisms.**

Whilst the total diversity of form, function and environmental resilience exhibited by organisms is awe-inspiring, each individual (and, to a slightly lesser extent, each species) operates within a relatively narrow range of constraints. Constraints fundamentally take two forms, (i) physical and (ii) evolutionary. Evolution can never reach 'perfection' because of these constraints and organisms are essentially hotchpotches of numerous compromises.

Rule 9**Chance is important.**

Chance events play a critical role in ecology. The opening of a gap in a forest canopy or the breaching of a sand dune after a storm will have a major impact on the ecology of the local fauna and flora, but both are unpredictable in either time or location. The role of chance is also integral to the evolutionary past of organisms. The importance of chance events in ecology does not mean ecological patterns are wholly unpredictable, but it necessarily places boundaries on the potential level of predictive detail.

Rule 10**The boundaries of ecology are in the mind of the ecologist.**

Ecology is a broad science, covering both organisms and physical environments and hence excludes little as potentially relevant. Mathematics, chemistry and physics are tools essential to the understanding of ecology.

What are these rules?

The authors' experience of teaching ecology, and the relayed comments of their colleagues, has given them insight into some common pitfalls which ecology students make. This set of rules is designed to counter these pitfalls and set students on the right course. The list is neither comprehensive nor mutually exclusive, but we hope will nevertheless serve as a useful guide.

Rule 1***Ecology is a science***

Ecology is a purely scientific discipline which aims to understand the relationships between organisms and their wider environment. Like any science, the outcomes of ecological studies do not dictate ethical or political actions. It is important to make this distinction because the environmental movement has endowed the word 'ecology' with political connotations. It is right that ecology should inform politics, but as a student of ecology it is imperative to consider ecological research from a rigorous scientific viewpoint.

Rule 2*Ecology is only understandable in the light of evolution*

The huge diversity of organisms, and the wealth of variety in their morphologies, physiologies and behavior are all the result of many millions of years of evolution. This evolutionary history has left an indelible impression on each and every individual. It is only possible to make sense of the patterns we find today in the light of this evolutionary legacy.

For example if we want to understand why the ostrich, emu, kiwi and rhea are all flightless (an unusual condition in birds), it is critical to know that these birds all share a common ancestor which was flightless, and that the species above became separated on different continents by the break-up of the ancient continent Gondwanaland. Therefore, looking for an independent adaptive reason for flightlessness in each species would be flawed.

At a wider level, the tendency of evolution to optimize organisms' fitness (although see Rule 8) provides ecologists with a valuable tool in hypothesizing organism structure and behavior. Thus, the large size of the peacock's tail suggests that males with larger tails have higher levels of fitness – and indeed data supports this hypothesis.

Some authors have suggested that the environment is the fundamental constraint on organisms and that ecology can more-or-less ignore evolution and genetics. This is a clear misinterpretation of the evidence – there is now ample evidence of short-term evolutionary changes which affect ecological patterns. Some of the best documented examples are the evolution of resistance to pesticides in crop pests and antibiotics in bacteria, and similar patterns have been observed in natural systems. Further, genes control every aspect of an organism, including the way it responds to the environment, so they must be the dominant component. Ecologists considering the behavior of animals should understand that animal behavior is controlled by genes just as much as gut enzymes are. There are now many examples where genes for behavioral traits have been identified.

Rule 3*Nothing happens 'for the good of the species'*

A common misconception is the notion that patterns of behavior in organisms which appear to be **costly to an individual** (for example the dying of a female octopus immediately after giving birth or the defensive suicidal attacks of some soldier ants) are '**for the good of the species**'. This argument is absolutely and completely wrong, and only advanced by those who failed to grasp the importance of Rule 2. Natural selection will favor those genes which are passed on to the most offspring. If the genes for suicidal behavior in ants or early death in octopuses were good for the species but bad for the individuals carrying them, evolution would favor their replacement with other genes. Equally fallacious, for the same reason, is the argument that population size is limited via reduced birth rates 'for the good of the species'. Both altruism and population regulation are easily understandable in terms of evolution acting on individuals.

Rule 4*Genes and environment are both important*

The environment an organism finds itself in plays an important role in determining the options open to that individual. Environmental conditions will define the birth rate, growth rate and level of mortality of a species. However, the genes which define an organism's makeup are also of fundamental importance. The emergent phenotype of an organism is a joint product of its genetic code and the environmental stimuli that affect it during development:

environment + genotype => phenotype

To understand ecology it is important to appreciate the fundamental nature of both of these factors, and the fact that they interact.

Rule 5

Understanding complexity requires models

At face value, ecology might appear incomprehensible – millions of species, each with varying numbers and ever-changing behaviors set in the context of a structurally complex and dynamic environment. Clearly, we cannot understand it all at once. The solution is a two-step process, firstly to identify a small and **specific question**, such as ‘why do male blackbirds form territories?’, and then to test a **specific hypothesis**, for example ‘male blackbirds with a territory have a better chance of getting a mate’. What we have done is to construct a verbal model of the world, which we then set about testing. —

Sometimes, the model we want to test is more complex, such as ‘when collecting food for its nestlings, a starling needs to consider both how far away the nest is and how difficult it is to forage with a beak full of worms’. Starlings become slower and slower at catching prey as their beaks become fuller, but if the nest is a long distance away, it is worth spending more time catching prey. When we have a **complex model** like this, it is best to frame it in terms of simple mathematics otherwise ambiguities and confusions are easily introduced. The predictions of a mathematical model of starling foraging behavior and some data from real starlings are shown in Fig. 1. The model appears to provide a good description of starling behavior, quantifying the degree to which starlings increase the load of prey as the distance to the foraging ground increases. Simple (and more complex) **mathematical models** are now widely used in ecology. Even complex models usually have a simple verbal explanation. This book employs a minimum level of mathematics, but remember that such models are integral to ecology.

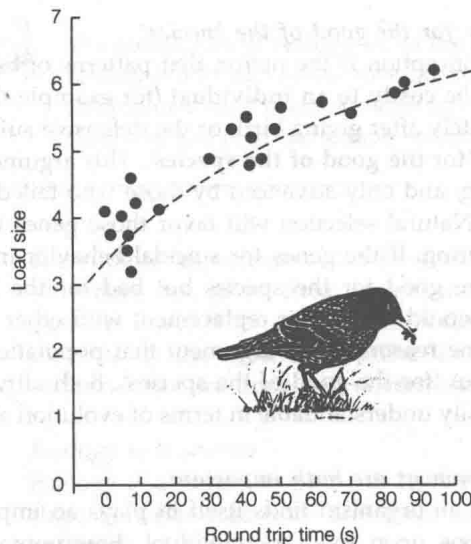


Fig. 1. The application of a mathematical model in ecology. The dashed line is the predicted relationship between the length of the round trip from nest, to foraging ground, to nest and the number of prey carried. The dots represent observations.

Rule 6***'Story-telling' is dangerous***

In attempting to explain ecological patterns or relationships, it is easy to slip into a make-believe world where every observation is readily explained by some *ad hoc* assertion, such as a classic examination blunder, 'polar bears are white so they are hidden from predators in the snow' (the problem being, obviously, that there are no natural predators of polar bears). Such errors are not restricted to undergraduates – they are commonplace in popular natural history writing and films. Creativity should be encouraged in scientists at the level of constructing hypotheses. Indeed, an imaginative and probing mind is essential. However, the temptation to advance such hypotheses as facts should be avoided.

Rule 7***There are hierarchies of explanations***

For any observation there is often an immediate cause that can be diagnosed. Often this causal explanation is insufficiently informative and we need to probe deeper to gain a fuller grasp of the situation. For example, a radio-tagged mole was found to have been stationary for three days. The proximal explanation of this was simple – it was dead. Further investigation found that it had a high density of gut parasites, which were the likely cause of death. It may have been possible to further investigate whether the mole was genetically predisposed to parasite infection or whether the environmental conditions had favored parasite survival, or some further explanation. The level of explanation required depends on the question being asked. For example, we might ask 'Why do males of many duck species adopt a bright or high-contrast breeding plumage?' The immediate causal explanation is that testosterone levels rise in spring and cause the changes. For an ecologist, this explanation is insufficient, but a fuller explanation is rooted in the fact that drakes with dull plumage generally have low mating success. Clearly there are further explanations beyond this ('Why do dull drakes fail?', 'Why do drakes show seasonal plumage variation when many birds do not?'). The point is that even if a phenomenon is 'explained' there may well be further explanations which shed a different light on the observation, without the original explanation being in any way wrong.

Rule 8***There are multiple constraints on organisms***

Whilst the total diversity of form, function and environmental resilience exhibited by organisms is awe-inspiring, each individual (and to a slightly lesser extent, each species) operates within a relatively narrow range of constraints. Constraints fundamentally take two forms, (i) those imposed by the laws of physics – **physical constraints** – and (ii) those caused by the vagaries of evolutionary history and the limitations on genetical flexibility – **evolutionary constraints**. Physical laws dictate what is and is not possible for organisms to achieve. Thus, it is not possible for an elephant to have the limb proportions of a gazelle, because, whilst an elephant is only roughly four times as long as a gazelle, it is about 64 times the weight (and hence needs limbs 64 times stronger), because volume (and hence weight) increases cubically as length increases linearly ($4^3 = 64$). There is thus a **trade-off** between nimbleness and large size. Similarly, there is an upper size limit on single-celled organisms, such as bacteria, which rely on diffusion over their outer surface to uptake assimilates, because as the size of an organism increases, the volume increases more rapidly than the surface area. Big bacteria would not be able to transfer assimilates to their centers. Physical constraints thus impose ubiquitous trade-offs.

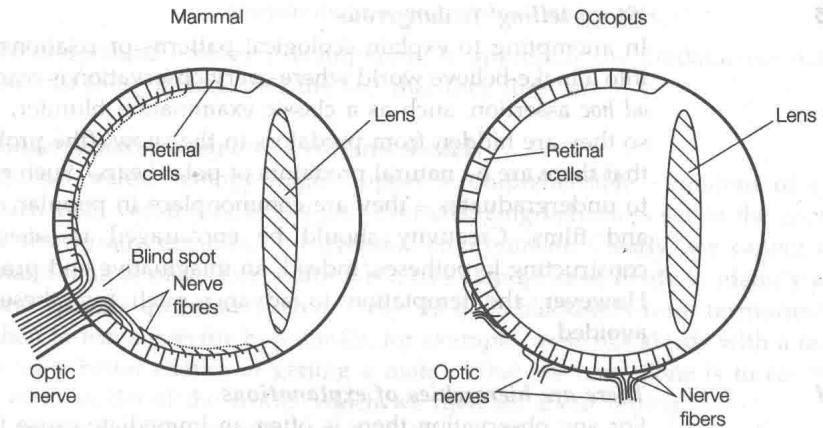


Fig. 2. A diagrammatic comparison between the eye of an octopus and that of a mammal, indicating how different evolutionary histories have produced a blind spot in mammals but not in octopuses. The size of the retinal cells is greatly exaggerated.

Evolutionary constraints are equally ubiquitous, but much less predictable. For example, the blind spot in the vertebrate eye occurs because of a basic design fault – the nerve connections of the photoreceptive cells are on the inner edge of the retina (the side which the light hits) and nerve fibers merge, forming the optic nerve, and exit the retina together. At this spot no light can be detected, resulting in a zone of missing vision – a blind spot. There is nothing inevitable about this arrangement, and indeed in the octopus (a mollusc, which evolved advanced eyes independently of vertebrates) the retinal cells are the ‘right’ way up, with nerve connections on the outer edge (Fig. 2). Where the nerve fibers merge to form the optic nerve, they are already on the outer edge of the retina and so there is no blind spot. Another example is that of the laryngeal nerve, which in fish passes directly from the brain to behind the sixth gill arch. During evolution, the gill arches have been transformed and the sixth gill arch in mammals is now represented by a blood vessel near the heart. The result is that in mammals the laryngeal nerve takes a detour, going from the brain to the heart and returning to the larynx. In long-necked mammals, such as giraffes, this detour is considerable. A much better design would be a direct connection from brain to larynx, but evolution has not offered this opportunity.

Evolution can never achieve ‘perfection’ because of these constraints and organisms are essentially hotchpotches of numerous compromises, despite the many examples of amazing design.

Rule 9

Chance is important

Chance events play a critical role in ecology. The opening of a gap in a forest canopy after a storm will have a major impact on the ecology of the fauna and flora of the forest floor, but it is unpredictable in either time or location. Similarly, the dynamics of sand dune and rocky shore species is dominated by the random destruction and creation of new, bare colonizing surfaces. The population decline of the passenger pigeon, which was so numerous in North America in the eighteenth century that flocks passing overhead blocked out the sun for minutes at a time, was largely caused by over-hunting. However, extinction was finally caused by the chance combination of disease and a harsh winter. The role of chance is also integral to the evolutionary past of organisms, as the