精要速览系列

Instant Notes 先·锋·版

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

Ecology

生态学

（第二版）

影印本

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内 容 简 介

"精要速览系列(*Instant Notes Series*)"是国外教材"Best Seller"榜的上榜教材。该系列结构新颖,视角独特;重点明确,脉络分明;图表简明清晰;英文自然易懂,被国内多所重点院校选用作为双语教材。先锋版是继"现代生物学精要速览"之后推出的跨学科的升级版本。

本书是该系统中的《生态学(第二版)》分册,全书共24章,介绍了环境中各因素的作用、种群生态学、生物竞争、寄生和互生、群落和群落动力学等,新版在第一版的基础上内容进行了全面修订和扩充,增加了该领域的最新发展和前沿。

本书是指导大学生快速掌握生态学和环境科学基础知识的优秀教材,也是辅助教师授课的极佳教学参考书,同时可供相关专业的研究生参考。

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

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ABBREVIATIONS

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

Aulay Mackenzie, Andy Ball and Sonia Virdee

To Ishbel, Eilidh, Sara, Simon and Katrina

CONTENTS

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 availablity, 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.

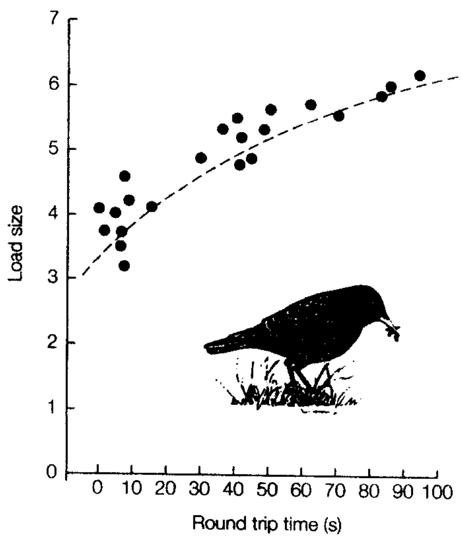

Fig. 1. The application of a mathematical model in ecology. The dashed line is the predicted relationship between the length of the round trip from nest, to foraging ground, to nest and the number of prey carried. The dots represent observations.

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.

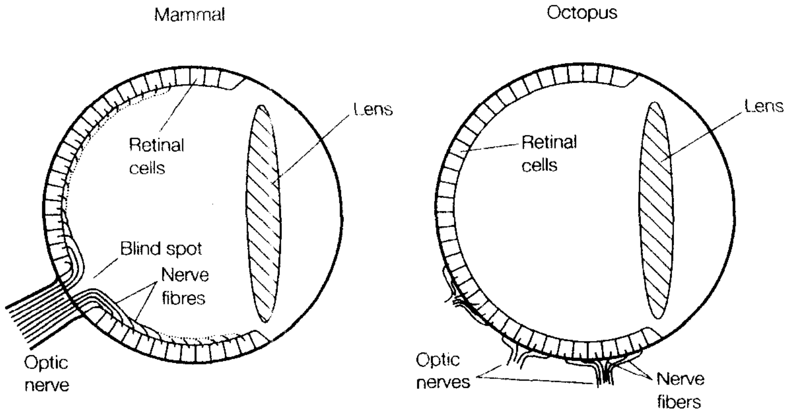

Fig. 2. A diagrammatic comparison between the eye of an octopus and that of a mammal, indicating how different evolutionary histories have produced a blind spot in mammals but not in octopuses. The size of the retinal cells is greatly exaggerated.

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 (*Ectopistes migratorius*), 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 and subsequently, diminished breeding success at low population densities. 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 blind spot of the vertebrate eye (see Rule 8 and *Fig.* 2) illustrates. 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

A science which covers both organisms and physical environments necessarily excludes little as potentially relevant. Of course, few ecologists have direct need for an understanding of astrophysics or the behavior of quarks, but, depending on the question studied, it may be essential to understand, for example, the chemistry of clay when investigating the availability of nutrients to plant roots or the physics of flight when studying the energetics of hummingbirds. A good ecologist regards mathematics, chemistry, physics and other disciplines as tools essential to the understanding of ecology.