The Song of the Dodo: Island Biogeography in an Age of Extinctions Study Guide

The Song of the Dodo: Island Biogeography in an Age of Extinctions by David Quammen

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Plot Summary

The Song of the Dodo is David Quammen's journalistic account of the development of the branch of ecology called island biogeography and an examination of how its theories might be applied to modern conservation efforts. Part scientific explanation and part travelogue, Quammen escorts his readers through the sometimes bitter infighting among ecologists and takes them island hopping around the globe to look at real cases of ecosystem decay.

Island biogeography is the study of the distribution of species in island habitats. Islands make useful case studies, Quammen explains, because their isolation and size make it possible to examine the entire system. Looking at what species survive or go extinct and how species evolve and change on islands can provide, in theory, practical information on what a species requires to remain viable into the future.

Quammen traces the origins of island biogeography to the pioneering work by Charles Darwin and the lesser known but equally important Alfred Wallace, both of whom based their theories on research performed on islands. He highlights the major shifts in thinking about evolution and the development of species in the years since Darwin and Wallace and brings the science up to the present day, interviewing several leading ecologists and conservation officials and outlining the major modern lines of thinking about the practical application of ecological theory. It is a field rife with conflicting ideas and Quammen delves into the personalities behind the most contentious areas of the subject.

Islands are not necessarily surrounded by water, Quammen points out. Sections of rainforest can become islands when they are isolated by clear-cutting and river habitats can become islands when damming isolates them from one another. As natural habitat on the mainlands of the world becomes more and more disjointed, Quammen argues, the lessons of survival and extinction taken from islands become globally applicable. One central question that arises pertains to the best design for natural preserve areas and Quammen explains the controversy over whether it is better to create single, large reserves or several smaller reserves.

Interspersed with Quammen's explanations of the scientific theories are his personal accounts of his travels around the world while researching his book. He recounts the hunt for a supposedly extinct species of lemur in Madagascar and the restoration of the nearly extinct kestrels on the island of Mauritius. In the final chapter, he retraces the steps of Alfred Wallace to the South Pacific island of Aru to find the extravagant and rare bird of paradise called the cenderawasih.

Quammen concludes his book on a hopeful note that despite the ever-expanding encroachment of man on the world's natural habitat, a way will be found to preserve the natural diversity of the world's species.



Thirty-Six Persian Throw Rugs

Thirty-Six Persian Throw Rugs Summary and Analysis

The first chapter is a brief introduction to Quammen's main subject, the division of the natural environment into isolated pieces that act as virtual islands. As a metaphor, he asks the reader to imagine a large and elaborate Persian rug that has been cut into thirty-six pieces. Each piece is equally complex and well made, but the overall pattern has been ruined and the edges begin to fray.

This fraying is analogous to the unraveling of ecosystems as they are divided into smaller and smaller pieces by deforestation, development, damming and other human activities. Understanding how these small ecosystems behave is therefore an important part of future conservation efforts, Quammen argues. We can better understand how they behave by looking at naturally small ecosystems, namely, islands.



The Man Who Knew Islands

The Man Who Knew Islands Summary and Analysis

Quammen begins his examination of island biogeography by briefly introducing some of the key figures in its development. Island biogeography is important, he explains, because the small size of the ecosystems on islands make the evolutionary processes very pronounced. It is a field that was around even before the subject had a formal name. Charles Darwin, one of the developers of the theory of natural selection based his ideas on data collected from island species in the Galapagos Islands in the 1850s, Quammen notes. At the same time Darwin was developing his theory, a man named Alfred Wallace was coming to the same conclusions while studying island species in the Malay Archipelago. This started a trend in island studies that continued for the next hundred years.

In 1967, an important book was published entitled, "The Theory of Island Biogeography." Written by two young scientists, Robert MacArthur and Edward Wilson, "The Theory of Island Biogeography" became an important text on the subject and set the course for much of the research being done currently. Quammen will return repeatedly to this work later in the book.

Always curious about nature, Wallace educated himself by reading library books and collecting beetles with his friend, Henry Bates. Insect collecting was a popular hobby among the wealthier classes in England, and the two eventually embarked on an enterprise to travel to the Amazon River region of South America to collect exotic insect specimens that would be shipped back to London and sold at a profit.

Once in South America, Bates and Wallace split up to cover more territory. Wallace faced significant hardships in the Amazon jungle, but developed survival skills and a sharp eye for spotting small differences between the species of insects and birds he collected and preserved for later sale in England. He took extensive notes and began to think deeply about what might cause different species to arise. Unfortunately, nearly all his notes and specimens were lost as he was returning to England when the boat he was on caught fire and sank, leaving him and several of the crew in a lifeboat for several days before being rescued.

Wallace produced two books about his journeys in South America and began to think about the origins of the various species he had observed. The skills Wallace developed in the Amazon rainforest served him well when he decided to travel to the Malay Archipelago, in what is now called Indonesia, where he went to gather data to research the species question.

Theories about the origin of species at this time ranged widely. Darwin had not yet published his revolutionary text and most theories were still based partly on religion. The "special creation theory" was one such notion. It held that God created each



different species especially to fit its habitat and place in the larger scheme. Wallace challenged this idea, pointing out that the literal story of Noah's Ark could not have accounted for the dizzying number of individual species on the planet. He also noted that some ecological niches went unfilled in some places, which seemed to contradict the idea that God had created an animal for every special purpose.

While examining bird species in the Malay Archipelago, Wallace observed apparent relationships between variant species. He noticed greater or lesser variances between islands. From his observations he developed a theory that species develop from similar species and appear in relation to them in time and place. Wallace, aware of the research that Darwin has conducted on islands, but unaware of the similar theory that Darwin had already developed but not published, wrote to Darwin explaining his discovery.

This put Darwin in a tough spot, Quammen explains. Realizing that Wallace had independently hit upon the same process of natural selection that he had, he turned to his friends to ask their opinion on what he should do. They advised him to quickly publish the outline of his theory to establish that he had already developed it. Darwin was reluctant, as he had not yet compiled al the support he wanted before publishing. In the end, Darwin composed a paper that was read at a conference of naturalists at the same time as one sent in by Wallace. Quammen dwells at length on the controversy in the subsequent years over whether Darwin acted honorably toward Wallace.

Quammen does not lay out Wallace's story in linear fashion. Instead, he jumps back and forth in the narrative of his life while presenting parallel passages that explain some of the concepts that Wallace had observed. One such concept was the difference between islands that had once been part of a larger land mass and those that had arisen in isolation, or had separated from a landmass so far in the past that the sepcies found there were very different from those found anywhere else.

Madascar is just such an island, and Quammen visited it to look at examples of the diversity of species found there. In particular, he looks at tenrecs, small shrew-like mammals that live nowhere else on the planet. On Madagascar, these tenrecs have divided over time into several different species in a process called "adaptive radiation." Quammen will return to Wallace and his studies in the Malay Archipelago throughout the book.



So Huge A Bignes

So Huge A Bignes Summary and Analysis

In the third chapter, Quammen introduces what he calls an "insular menu" of attributes that appear to be common to species that live on islands. He divides the list of attributes into those that apply to individual species and those that apply to island communities as a whole. The species attributes are as follows:

Dispersal ability

Size change

Loss of dispersal ability

Endemism

Relictualism

Loss of defensive adaptations

Archipelago speciation

Adaptive radiation

The community attributes he calls disharmony and impoverishment.

Quammen writes in a disjointed style, moving from subject to subject and returning to previous topics frequently. He addresses these attributes over the course of the chapter, interjecting personal stories about his travels to conduct research for the book and introducing scientists who are studying these various attributes of island biogeography.

Dispersal ability is the ability a species has to move from place to place. This is especially important in island biology where an island is newly formed, perhaps from undersea volcanic activity, and emerges with no life on it at all. It also comes into play when an island loses all its life after a catastrophic event.

This is what happened, for example, when the volcano Krakatau erupted in 1883, in the Malay Archipelago. The eruption devastated the entire island formed by the volcano, leaving only bare rock and rubble. Over the past decades since the eruption, Krakatau has provided science with a living experiment to watch how island habitats develop from nothing. Since it is isolated by sea, any new species to the island must be brought there somehow or immigrate there themselves.

The first animal reported to have arrived on the bare island after the eruption was a spider. Spiders have good dispersal ability, Quammen explains, as they are able to



release a length of silk and go flying aloft on air currents over great distances. Mosses, fungus and ferns were among the first plants, with their spores either carried by the wind or washed up in the surf. Fifty years after the eruption, one biologist counted 271 species of plants and animals living on the island, including a medium size monitor lizard. These species arrived by various methods. The first lizards probably swam or were carried their floating on logs or other material. Flying insects such as butterflies may have flown there, as well as bats and birds.

There are some species with surprising abilities to disperse, Quammen explains. The elephant, for example, currently the largest land animal on the planet, has been observed to swim great distances and some fossil evidence seems to suggests that ancestors of the modern elephant were dispersing onto islands long in the past.

Species that become established on islands often change in size over many generations, sometimes becoming very large or sometimes becoming dwarfed. This is the second item on the "insular menu." Some examples of this change include the komodo dragon, the largest lizard in the world which is native only to a few islands in Indonesia. On these same islands are fossil records of dwarf elephants, which one scientist, Jared Diamond, proposed had been the original prey for the komodo dragon, allowing it to thrive and grow to its great size over the course of many generations.

The mechanism by which species change size after becoming established on islands was examined in 1964 by a scientist named J. Bristol Foster, who compared mammal species on islands to their counterparts living on mainlands. Foster observed that once isolated on an island rodents tended to grow larger while large carnivores tended to get smaller. Large ungulates, like hippos, deer and pigs tended to get smaller. The reasons apparently were related to food supply and other factors. With less prev available on an island, large animals that need a lot of food will not survive well. Grass-eating species such as deer will expand to fill as much area as is available, but once they outgrow the supply, malnutrition might affect the size of their offspring and over time the species becomes dwarfed. Rodents, with fewer predators and less competition, might tend to get larger. Foster also proposed that because the gene pool in an island environment is contained, these changes will take place rather rapidly. This research by Foster is an important milestone in the study of island biogeography, Quammen explains, and his observations became to be known as the "island rule." Understanding of the mechanism behind it is later refined by a biologist named Ted Case, who expands the possible reasons a species might change size in an island environment.

When some species change size, they also lose their ability to disperse. This is especially true of insects and birds, it seems, and Quammen gives the dodo as an example as well as other flightless birds that are found on islands, like the kiwi and emu. For some of these species, like the dodo which is now extinct, this loss of dispersal ability created a biological dead-end. The dodo was confined to the island where it had evolved and could not escape.

Quammen defines the difference between endemic and relictual species, the next two attributes of island species. Endemic species are those that evolved in the same place



where they are currently found such as on an island. Relictual species are those that have survived in one place but disappeared from others.

Quammen next turns to the loss of defensive adaptations and uses flight as an example of one common attribute lost by many island species. Darwin had noticed that the beetles on the island of Madiera were unable to fly and theorized that flying on such a windy island might have become a disadvantage, as the beetles who flew were more likely to be swept out to sea, while those who did stayed on the ground were able to breed more successfully. Darwin also believed that traits that were acquired by a parent during its life were passed on to its young, however, which modern biology knows to be incorrect. Nevertheless, the observation of Darwin's that successive generations of a species can change based on its environment was correct.

The question of the flightless beetles was examined more thoroughly by a scientist named Philip Darlington, who examined the wing sizes of various species of beetles to determine what conditions might lead to flightlessness. He found that flightless beetles were more likely to be found living in dense populations where there was ample food within a small area and few predators. Without the need to cover large areas to find mates or food, and few predators to escape, these species simply did not need to fly in order to survive. Quammen quickly mentions the concept of "economy of resources" which holds that given a certain amount of life resource, a species will tend toward those adaptations that are most beneficial and away from those that are not. Over time, the resources expended on wings might be used toward stronger jaws or legs which might be more useful on the ground.

Other defensive adaptations that seem to be given up by many island species are wariness, short infancies and protective coloration. Early sailors noticed that the animals they found on islands were often very trusting and unafraid of humans, making them easy marks for food. Some birds nested and laid eggs out in the open, as there were few predators to bother them. The lack of large predators also seems to contribute to the loss of drab coloring that helps hide an animal. Many island species of birds and lizards are brightly colored.

Archipelago speciation is the process by which a species on an island expands by immigration to a nearby island and then over time the two populations evolve on different paths until they become different species. This occurs when there are islands that are close enough for occasional immigrations, but not so close that immigration happens frequently. This process contributes to the greater diversity of species on islands, and was observed by Darwin during his time in the Galapagos islands.

Darwin first became aware of the different species of similar animals on each island when the vice-governor of the islands told him that each island had a different type of tortoise living on it. He also noticed the same kind of variation among mockingbirds and finches.

It was the finches that became the most famous part of the Darwin "legend" Quammen writes. He then takes considerable time in debunking this myth by putting forth the



arguments of an author named Frank Sulloway, who noted that when Darwin was collecting specimens of finches he rarely tagged them with the location where they were found. Only after returning to England and after a colleague better versed in ornithology had sorted them out did Darwin strike on his theory of how they differed and what that meant about how they had evolved. This is a considerable departure from the main subject of the chapter and is similar in tone to the long digression of the second chapter in which Quammen advances the idea that Darwin receives more credit for discovering natural selection than he deserves.

Archipelago speciation is similar to adaptive radiation in that one line of a species diverges into different ones, however adaptive radiation takes place within the same environment where there are isolated niches that can be filled. Quammen refers again to the tenrecs of Madascar and also tells the story of the discovery of a species of bamboo eating lemur that had apparently diverged from other bamboo-eating lemurs to adapt the ability to eat the poisonous young shoots of the plant.

Quammen sums up these items on the "insular menu" as the highpoints of island biogeography, and turns to to the two larger community attributes, disharmony and impoverishment. Disharmony is a relative imbalance in the diversity of species that is found especially on islands. There are far more species of finches in the Galapagos for a given area than on the nearest mainland, South America, for example. Disharmony also refers to the difference between islands and the other masses of land they were once associated with. Islands that are fairly young and have not been isolated for long will not have much disharmony from their related neighbors. Islands that have been isolated for a long time, such as Madagascar, will show considerable disharmony from other areas.

Impoverishment, which is a kind of disharmony, refers to the fact that islands support fewer species altogether than larger mainlands. Darwin had noticed this, and it was further examined as the "species-area relationship" that Quammen will examine in more detail later in the book. It also refers to the process of extinction, which is more common among island populations than mainland ones. This question of extinction is so important, Quammen argues, that it deserves a deeper look.



Rarity Unto Death

Rarity Unto Death Summary and Analysis

The dodo, a large pigeon-like bird, once lived on the island of Mauritius in the Indian Ocean. It could not fly, and nested on the ground. It apparently ate fruit that dropped to the ground from trees. This, Quammen writes, is about all that is known for certain about the dodo, which went extinct some time in the late 17th century. It was described by sailors as a stupid bird that did not try to escape humans and which, while not the tastiest of meat, provided stopping ships with a source of food. Their large eggs were also gathered and eventually the numbers began to dwindle.

Human hunting certainly hurt the dodo population, Quammen explains, but there appears to be more to the story. A species of monkey and pigs had also been introduced to the island by sailors and had established themselves in great numbers. Quammen speculates, although he offers no evidence, that these omnivorous animals might also have contributed to the extinction of the dodo.

The species of monkey that became established on Mauritius is called a crab-eating macaque and is still common there. Quammen visited Mauritius to a facility where an Australian man named Owen Griffiths raises them to use in medical research. Quammen went to Mauritius to see a biologist named Carl Jones, who had a project trying to rescue the population of another rare Mauritius bird, the Mauritius kestrel. Quammen will return to Jones' project later in the book.

Islands are common sites of extinction, Quammen explains, and turns to the example of Tasmania, an island off the coast of Australia. Tasmania had once been attached to the mainland of Australia and shared many of its species, but in the thousands of years since it became isolated by water a few species had developed that were only found on Tasmania. One of these was the "Tasmanian tiger," and not a tiger at all, but a predatory marsupial that resembled a dog and had distinctive stripes. From its scientific name, Quammen calls it a thylacine.

The British established a penal colony on Tasmania in 1802 and found the thylacine present at that time. It had been known for ages by the aboriginal people who lived in small tribes on the island and appeared in their art. As the British expanded their colony, they began to clear land and raise sheep, which the thylacine sometimes killed. A bounty was placed on thylacines and over the course of several years, they were hunted to extinction, or at least that is what was assumed for years. In recent times, Quammen writes, reports of sightings of animals that sound like thylacines have been reported on Tasmania. It may be possible that some have survived in small numbers over the past 150 years or so. Quammen went to Tasmania and spent a night out in the Tasmanian wilderness in hopes of possibly seeing one, but he does not.



Quammen also tells the long story of the aborigines of Tasmania, who, like the thylacine, were essentially hunted into extinction. They had lived in small tribes on different parts of the island and sometimes raided British outposts. The British established reservations for the aborigines and forced them to relocate. Some were converted to Christianity and convinced to come out of the forest to live in houses. The reservations were squalid and eventually the population of aborigines declined until only one single Tasmanian aborigine was left alive, a woman named Truganini. She died in 1876.

Quammen also went to the island of Guam, to visit a biologist who is studying the effect that an introduced species of snake is having on the local bird population, specifically on a species called the Guam rail. The rail, along with several other bird species, began to decline and at the same time an exotic snake not native to the island began to explode in population. Quammen introduces the concept of the "trophic cascade," which is when the increase or decrease of a population has a direct or indirect effect on other species. A rising population of snakes that eat bird eggs might make the bird population go down. Fewer birds might mean that fewer insects are eaten, allowing the insect population to rise. More insects may have an impact on the plants they use for food, and so on in a cascade of effects. This is especially visible on islands.

Quammen closes the chapter on extinction with a reference to the work of a scientist named Michael Soule, who studied island-dwelling lizards in the Gulf of California. Soule identified eighteen potential contributing factors to the extinction of a species, including rarity and loss of habitat. One of Soule's most disturbing observations, according to Quammen, was that the number of extinctions observed in recent years had risen, especially on islands, and that it was becoming more common to find them occurring on mainlands.



Preston's Bell

Preston's Bell Summary and Analysis

The relationship between the area of an ecological system and the number of species it supports is one that has been examined for many years, Quammen explains, with different conclusions. As it is related to island biogeography, the simplest explanation of the relationship is that the larger the island, the more species it can support.

This seems intuitive, Quammen writes, but it is more complicated than it first appears. He describes the observations of a biologist named Philip Darlington, who noticed that there seemed to be an approximate mathematical ratio between the area of an island and the number of species of related animals found on it. Darlington looked at amphibians and reptiles and noticed that an island of about four square miles had about 5 species from these groups. An island of ten times the size or forty square miles held ten species. An island of 4,000 square miles had 40 species and so on. Multiplying the area times ten apparently doubled the number of species supported.

Another researcher named Frank Preston made similar observations, and also made note of the distribution of species within island habitats. Preston noticed that by plotting species in a graph based on their relative commonness, a bell curve was produced. In other words, in any ecological system there are a few species that are very rare, many species that are somewhat common, and a few that are very common. Preston also observed that the few most common species made up the bulk of the actual individual animals.

From these observations, Preston made a practical assertion, which is that if his observations held true for all ecological systems, as he believed they did, it would not be possible to create in a small area such as a national park or nature reserve, a "replica" of a system that originally took up a large area.

Quammen explains the difference between an "isolate" and a "sample." A sample is a defined area of a larger system that is looked at by biologists to provide data that can be extrapolated to the larger system. An isolate also a defined area, but it stands alone, unconnected from any surrounding system. An island is an isolate, but isolates can also occur on land. He returns to his description of the nature parks of Indonesia where the komodo dragon still lives, They are on islands, but are also surrounded by development by humans. The komodo habitat has become an island within an island.



The Coming Thing

The Coming Thing Summary and Analysis

Quammen returns to the important work by Edward Wilson and Robert MacArthur regarding the balance of island species. Wilson and MacArthur postulated that extinction was a regular occurrence in island habitats, as was the immigration of new species. In a paper entitled "An Equilibrium Theory of Insular Zoogeography" published in 1963, Wilson and MacArthur laid out their postulation that the rates of immigration and extinction would tend toward a balance, or equilibrium, where new species were introduced at about the same rates others went extinct. The theory presented in the paper was then expanded into a book called "The Theory of Island Biogeography." It was a book that "changed things," Quammen writes (pg. 415.)

MacArthur died a few years after the publication of the book, but Ouammen visited with Edward Wilson to interview him about his important theory. Wilson presented Quammen with a slide show outlining how the two men had developed their idea about island habitats. They had started with the species-area relationship that had been described earlier by Preston. They tied this to the observation that fewer species were found on remote island than on less remote islands. Before this, scientists had explained this disparity in terms of time. Remote islands would take more time to colonize because of their distance from other land, their predecessors had thought. Wilson and MacArthur believed this was not the reason, because some remote islands had fully-developed ecosystems that had been active for a long time, but still supported fewer species. They argued that it was immigration and extinction that determined the number of species on an island, and that this number could be predicted by taking into account of the size and remoteness of a particular island. Using their theory, they made a prediction about the island of Krakatau that had been wiped of all life and had then been recolonized by plants and animals. They predicted that the data collected from Krakatau would show that it would have an equilibrium of thirty species, that it would have taken forty years to reach equilibrium, and that it would have a turnover of one species per year. They found that the data matched fairly closely their predictions.

It was only one island, however, and Wilson wanted more data. He conceived a project along with a graduate student named Dan Simberloff that would allow them to directly test the theory. In the Florida Keys were many very small mangrove islands that supported populations of mainly insects. They selected some of these small islands, covered them with tarps, and fumigated them to kill all the insects on them, then returned regularly to measure the recolonization rate. They found that the experiment supported the theory. The more remote islands colonized at a slower rate and supported fewer species than the less remote islands.

Part of the reason this theory was so important, Quammen explains, is that the authors recognized that it was also important for mainland populations. Islands are only one



kind of isolated habitat. Mountaintops, caves, lakes and other naturally isolated regions exist throughout the world, and the theory of equilibrium ought to apply to any of them.

It also had repercussions in the area of conservation, where natural habitat is set aside as a reserve. Deriving his ideas from Wilson and MacArthur's theory, Jared Diamond proposed a set of guiding principles in the design of nature reserves. Put simply, the larger the reserve and the closer it is to other reserve areas, the more species it will be capable of sustaining. These principles would be hotly debated over the coming years, Quammen explains, as scientists fought over whether a single large reserve was always better than several small reserves. The question became known by the acronym SLOSS, standing for "Single Large Or Several Small."



The Hedgehog of the Amazon

The Hedgehog of the Amazon Summary and Analysis

The theory that one large reserve would support more species than several small ones was challenged in a paper by Dan Simberloff and Lawrence Abele published in 1976. They argued that the theory had not been widely tested, and the conclusions did not always seem to follow from the original equilibrium theory. Abele, who studied heads of coral that supported small contained ecosystems, found that two small coral heads supported more species than one large one of equal area, for example, apparently contradicting the design guidelines. They proposed that competition, the dispersal ability of species and the number of species might all contribute to natural situations where smaller areas might support more species than larger ones.

The paper by Simberloff and Abele set off a raging debate in the field, Quammen explains, with ecologists coming down on different sides of the question of the practical application of the prevailing theories in designing natural habitat reserves. One person interested in the outcome of the debate was Thomas Lovejoy, who as a program director for the World Wildlife Fund had the job of actually trying to create natural reserves.

Lovejoy conceived a project that would examine the question in a controlled experiment. Working with Brazilian government, he convinced Brazilian ranchers who were clearing rainforest to create rangeland to leave square reserves of rainforest standing in determined sizes. These islands of rainforest were then studied, and the species counted to see if an ideal size could be determined. Quammen visited some of these sites with Lovejoy as the project was still underway. It had not come to any hard conclusions, but had noticed that the smallest of the reserves had fairly quickly unraveled, unable to support their former populations.

In support of the "single large" model, Quammen cites the work of a doctoral student named William Newmark. Newmark looked at historical records of wildlife sightings in U.S. national parks over the past several decades and compared the number of species with various attributes of the parks, including the area. He found that the area of the park had the highest correlation to the number of species present.



The Song of the Indri

The Song of the Indri Summary and Analysis

The indri is a large and unusual lemur that lives on Madagascar. It lives its whole life in trees, jumping from trunk to trunk in acrobatic leaps. It has a distinctive cry that is one of the loudest of any animal, traveling for over a mile through the dense forest where it lives. The animals are reclusive and wary of humans. Quammen went to the region of Madagascar where the indri live in a special reserve. Taking a hotel room, he hired a local guide, a young man named Bedo, who was a self-taught expert on the wildlife of the area and had a reputation among scientists studying the ecology of Madascar as an indispensable guide for tracking animals. Bedo took Quammen into the reserve and helped him locate an indri. Quammen writes a good deal in this chapter about Bedo and his love for the forest, and about his tragic death in his home village. The details of his death are unclear, Quammen writes, but his body was found in a river and it is believed he was murdered. His success making money as a guide may have raised jealousies among the other residents of the village, Quammen speculates.

Nobody knows exactly how many indri are still living in Madagascar, Quammen explains, so it is difficult to tell what their future might be. He introduces the concept of a "minimum viable population," first raised in a journal article by A.R. Main and M. Yadav in 1971. The minimum viable population is the theoretical minimum number of individuals of a species required for that species to avoid extinction. Several papers followed that examined the subject, and the question was expanded to look at the varying factors that might affect this minimum number.

The genetic history of a species was found to possibly play a role. Species that had been isolated for a long time already were probably more likely to have bred out most of the harmful genes that might crop up and endanger a high percentage of the individuals. As the population of a species dwindles, the likelihood of animals breeding with close relatives becomes higher, raising the probability of genetic problems. Random chance might produce significantly more males than females in a generation, suddenly reducing the number of offspring in the next. Natural disasters might wipe out large areas of habitat suddenly.

A working definition of a minimum viable population would have to take all of these possibilities into account, and would be different from species to species. And then there was the question of what was meant by the term "viable." Scientists differed on what limits to use. One, Mark Shaffer, defined "viable" as "having at least a 95% chance of remaining extant for 100 years" (pg. 519.) He based his definition on his work examining the disappearing habitat for grizzly bears. Another scientist, a geneticist named Ian Franklin, along with Michele Soule, came at the problem from a genetic standpoint. They estimated that to avoid harmful inbreeding, a species required a population of at least 50 productive individuals. To maintain long term genetic adaptability, a population of 500 was estimated to be the minimum number. This became known as the 50/500



rule, Quammen explains, and was controversial among scientists and sometimes misapplied by agencies overseeing conservation projects, which would give up trying to save a species once its numbers dropped below 50.

Quammen intersperses his discussion of the minimum viable population question with long descriptions of the beauty of Madagascar and his experiences staying there and visiting the forest with Bedo. He dwells on Bedo's death and gathers the sad reactions of the scientists who had worked with him.



World in Pieces

World in Pieces Summary and Analysis

Quammen brings the main theme of his book back around in this chapter, reminding his reader that these questions formed to study the biology of islands now apply to mainlands as well, where ecosystems are being divided into virtual islands by human activity, and looks for some real-world examples of how the lessons of island biogeography are being applied.

Quammen returns to the efforts of Carl Jones to save the Mauritius kestrel. The Mauritius kestrel population started declining rapidly in the 1950s and 60s, and by the 1970s it was estimated by one scientist that only four individuals were still living. The cause was habitat loss and possibly predators that ate kestrel eggs as well as pesticide poisoning. A group called the International Council for Bird Preservation stepped in to study the kestrel and counted eight individuals in 1973, two of which disappeared shortly afterward, leaving just two breeding pairs and some non-breeding individuals. One pair was captured to attempt to breed them in captivity, but they did not breed successfully. Meanwhile a cyclone wiped out much of the existing kestrel habitat on Mauritius, further stressing the population. By 1978 there was still only one wild breeding pair.

Carl Jones was sent to Mauritius to shut down the project, but he not give up on the bird. He took the risky move of taking some wild eggs from a nest and incubating them in his lab, hoping that the kestrels might lay a new clutch once they found their first one missing. Working from his lifelong experience breeding birds, he soon showed signs of success incubating the eggs safely in his lab away from predators. By choosing the healthiest of the birds he hatched for future breeding, he avoided problems from inbreeding. He released birds into the wild and supplemented their food by feeding them mice, which he would throw up into the air for the kestrels to swoop down and catch in mid-air. Eventually he was able to get funding from other foundations to help him continue to restore the kestrel population.

Quammen followed Jones on a treacherous climb to examine several kestrel nests perched high on rock faces. Jones had set traps near the nests to capture any predators that might eat the birds or their eggs. In one trap they find a mongoose, a non-native species that preys on the birds. Jones kills the mongoose in a dramatic fashion.

The case of the Mauritius kestrel is promising, Quammen suggests. He quotes Carl Jones, "If you can save the Mauritius kestrel, you can save virtually anything" (pg. 567.) Quammen qualifies Jones' remark, however, by adding that the Mauritius kestrel has been an island species for a long time and never had a large population to begin with. It is a different matter with mainland species that once had large populations that then become isolated and start to dwindle.



Qammen gives the example of the muriqui, a large monkey that had once been abundant in the jungles of Brazil, but whose habitat had been separated into smaller sections. Unlike the kestrels on Mauritius, the genetic history of the muriqui had not played out on an island and so it had not bred out as many harmful genes. Suddenly reduced to a smaller population, the likelihood that these genes would arise to cause problems was increased. Quammen traveled to Brazil to visit a scientist named Karen Strier, who had studied the muriqui for several years. She explained to Quammen that the muriqui were highly endangered and now lived only in a few isolated areas. Proposals had been made to relocate the known populations of muriqui to a larger continuous area, but Strier was opposed to this kind of intervention. The two family groups she was studying seemed to be doing well in their own section of forest and she feared that relocating populations might do more harm than good. She was frank with Quammen that she knows others disagree with her. Quammen's point appears to be that it is not always clear, even among scientists, what the proper path to conserve a species should be.

Quammen turns to a practical example that unfolded in Texas. After hearing of the work of Michael Soule on minimum viable populations, an official from the U.S. Fish and Wildlife Service named Jim Johnson contacted Soule about a project that was being studied to create a reservoir at the confluence of two rivers on the Colorado River in Texas. The issue was that an endangered water snake lived in the rivers, and the reservoir would flood some of their habitat. Johnson was looking for some reliable data on how the dam would affect the snake and wanted Soule to study the problem.

Soule took on the project, along with a colleague named Mike Gilpin. They first discovered that the snake lived only in shallow riffles and they mapped these areas where they occurred. They next made estimates on how many individuals these riffles supported and how often snakes moved from riffle to riffle. Finally they looked at which riffles would disappear as the deeper water from the reservoir extended upstream and isolated the two branches of snake habitat on the separate rivers. They created a computer model using these factors and ran simulations. Their model predicted that with the dam built, the snake would probably survive at least 300 years into the future, but at a much smaller number of individuals, making it more susceptible to extinction from some other factor. The dam itself, they concluded, would not cause the snake to go extinct. They reported this, and the dam was built.

This chapter includes a wide digression by Quammen about his brief stay in Rio de Janiero on his way to visit Karen Strier, when he is mugged and spends the day in a Brazilian police station, unable to understand or speak Portuguese.



Message From Aru

Message From Aru Summary and Analysis

The final chapter is an optimistic epilogue in which Quammen describes his visit to the island of Aru, where Alfred Wallace had done his main research leading to his codiscovery of natural selection. Aru is still an isolated place and the only way Quammen was able to get there was to join a tourist cruise and to be let off on a nearby island, negotiating with the natives to take him out to Aru. He sought the bird of paradise or the colorful bird that Wallace had first described over a century before. He had heard there was a tree on Aru where the birds gathered to mate and the natives confirmed that there was such a tree. Guided by some of the natives, he made his way by boat to Aru and visited the tree, listening to the cry of the bird called the cenderwasih. Despite the signs of human activity even on Aru, the magnificent bird survives.



Characters

Charles Darwin

Charles Darwin was a British naturalist most famous as the developer of the theory of natural selection as the mechanism behind the origin of species. In a well-known book, "On the Origin of Species" published in 1859, Darwin outlined his theory that animals passed along adaptations to their offspring that became magnified and diverged in succeeding generations until they were so different that a new species existed. He based his theory on his observations collecting specimens in the Galapagos Islands. While his observations on the wide variety of finches on the islands is widely thought to be the origin of Darwin's realization, Quammen gives credence to authors who dispute that the finches played such an important role in Darwin's thinking.

At the same time Darwin was formulating his theory and refining it for publication, another naturalist named Alfred Wallace was coming to very similar conclusions. Darwin was aware of Wallace's ideas through letters he received from Wallace, and Quammen suggests that Darwin may have acted dishonestly toward Wallace in giving him proper credit for co-founding the theory. Quammen notes that Darwin's name is the one most usually associated with the theory of natural selection today.

Alfred Wallace

This is a British naturalist who discovered the process of natural selection independently of Charles Darwin at about the same time. Wallace left school as a young man and trained as a surveyor. He sought to educate himself about the natural world and nurtured a hobby of collecting beetles. Along with a friend, Wallace embarked on a trip to the Amazon River region of South America to collect exotic species of insects and animals and return them to England to sell. He lost nearly all his specimens at sea, however he found some success writing about his journeys.

Wallace had made careful observations about the apparent slight differences between similar animals in the Amazon, and went to the Malay Archipelago to further study exotic specimens. It was while there that he made the observations that led him to theorize that new species were always associated in time and place with similar species, and to realize this is because new species evolve from existing species.

Wallace entrusted his ideas to Darwin in letters, unaware that Darwin had already developed a similar theory about the same processes. His initial paper on the subject was presented at the same time as Darwin's at a meeting of naturalists in England. Later in life, Wallace engaged in some odd and unscientific beliefs, Quammen writes, which may be why he is not as closely associated with the theory of natural selection as Darwin.



Edward Wilson

This is the co-author, with Robert MacArthur of an important work on ecology called "The Theory of Island Biogeography" that proposed that the number of species in a given isolated area would approach an equilibrium where the number of new species was offset by the number of extinctions.

Robert MacArthur

This is the co-author, with Edward Wilson, of "The Theory of Island Biogeography" and co-developer of the equilibrium theory of island species. MacArthur died a few years after the publication of the book.

Carl Jones

This is a Welsh conservationist who successfully saved the endangered population of Mauritius kestrels from probably extinction by developing a program of captive breeding and release into the wild.

Thomas Lovejoy

This is a project manager with the World Wildlife Fund who set up an experiment in the rainforest of South America to study the effects of isolation on patches of forest of various sizes.

MIchael Soule

This is a biologist who studies the mechanisms behind the extinction of species. Soule identified eighteen factors that can contribute to extinction.

Michael Gilpin

This is a colleague of Soule's who helped develop a computer model to simulate the environmental effects of habitat changes on populations of animals.

Ernst Mayr

This is a biologist who studied the origin of species and emphasized the importance of geographical isolation in evolution.



Frank Preston

This is a theorist who observed that the numbers of species in a sample of habitat follow a certain pattern, with some very rare and some very common patterns, with most patterns falling between the two extremes. This pattern is called "Preston's Bell."

Rob Bierregaard

This is an ecologist who worked with Thomas Lovejoy at the World Wildlife Fund to study the optimum size for natural reserves.

Ted Case

An island biologist who studies a declining population of lizards on an island off the coast of Mexico.

Philip Darlington

This is a researcher working with beetle species who observed that larger areas apparently support a higher number of species.

Jared Diamond

This is a biologist who studied extinction and how the loss of one species can have indirect effects on many other species.

Ian Franklin

This is a researcher who proposed the "50/500" rule that stated that a species needs at least 50 productive individuals to avoid dangerous inbreeding and 500 individuals to avoid extinction.

William Newmark

This is an ecologist who studied the populations of large animals in US national parks to determine what effect smaller habitats had on them.

John Terborgh

This is one of the scientists who defended against Dan Simberloff and Lawrence Abele's challenge of the idea that one large natural reserve was better than several small ones.



Bedo

This is a native of Madagascar who teaches himself about the animals of the island and becomes a respected guide for visiting scientists. He is later apparently murdered.

Dan Simberloff

This is a conservationist who challenges the idea that one large natural reserve is always preferable to several small ones.



Objects/Places

Madagascar

This is a large island off the southeastern coast of Africa. Madagascar has been isolated for a long time and supports several species of animals found nowhere else, including tenrecs and lemurs.

Krakatau

This is a volcanic island in Indonesia that erupted in the 19th century, killing all life on the island.

Komodo

This is an island in Indonesia where the komodo dragon is found.

Mauritius

This is an island in the Indian Ocean where the dodo once lived. It is also the home to the endangered Mauritius kestrel.

Aru

This is a series of islands in the Malay Archipelago where Alfred Wallace gathered specimens for his research on the origin of species.

Brazil

This is a large South American country that has large areas of rainforest.

Tasmania

This is an island off the southeast coast of Australia that was once attached to the mainland. It is the last known location of the possibly extinct thylacine.

Guam

This is an island in the Pacific Ocean.



The Galapagos Islands

This is a series of islands off the west coast of South America where Charles Darwin first gather the specimens that led him to his theory on the origin of species.

Florida Keys

These are several small islands off the southern tip of the Florida peninsula.



Themes

The Fragmentation of the World's Ecosystems

The main ecological theme to Quammen's book is that the large natural areas of the world are being continually divided into smaller pieces, forming what are essentially islands of habitat just as isolated from one another as islands in the ocean. Island biogeography, which studies how species evolve and go extinct on natural islands, can show us what kind of impact we can expect on species that are isolated by this activity.

As an example of this kind of fragmentation, Quammen writes about the Brazilian rainforest where it is being cleared to provide pasture for cattle. This clearing can create isolated pieces of forest surrounded by grassland. Birds and flying insects may cross these clear areas, but other animals that rely on continuous tree cover will not. The smaller size makes prey and shelter to scarce for larger land animals and they disappear. This fragmentation also presents an opportunity for scientists who want data on what the optimum size is for nature reserves so that they might preserve the diversity of species originally found there. Quammen examines just such an experiment ongoing in Brazil.

While looking at islands can tell us how species arise and go extinct, Quammen explains, island species are sometimes different than mainland species in that they have evolved on islands and have had a long time to breed out harmful genes. Mainland species that go from large populations to small ones as their habitat is fragmented face genetic challenges as their gene pool is suddenly made smaller. This means that these mainland "islands" may be even more fragile than natural islands.

The SLOSS Debate

SLOSS stands for "Single Large Or Several Small" and refers to the question of what is the best design for natural reserves intended to preserve the diversity of species found in a habitat.

Several studies have observed a correlation between the size of an island and the number of species that exist on it. It has also been observed that remote islands generally have fewer species than islands that are closer to other islands or to mainlands. From these two observations about islands, some scientists have postulated that for the best preservation of diversity of species in a natural reserve a large uninterrupted area is the best design, as opposed to several small reserve areas.

While this seems almost obvious, Quammen explains, it is not a conclusion that is universally supported. Another group of scientists point out that there are observed cases in nature where several isolated habitats seem to have more diversity than larger ones of the same area. One study of undersea coral heads, for example, showed that several smaller ones had more species than a single larger one of the same area.



These scientists also point out that the theory has not been put to any real test and so the data does not yet exist to support it.

Quammen outlines the controversy over SLOSS and interviews some of the key figures on either side of the debate, as well as some scientists who have developed a study to test the theory by isolating patches of rainforest of graduated sizes to gather hard data on the relation between species and area.

The Importance of Extinction

The equilibrium theory of island biogeography was initially proposed by the scientists Edward Wilson and Robert MacArthur. It predicts that every island ecosystem will eventually approach a balance where the number of new species that arrive or evolve on the island will be roughly equal to the number that go extinct. Quammen makes much of this theory as it drives a good deal of the research into island ecosystems after its appearance.

Inherent in the equilibrium theory is the importance of extinction. It is a natural process, Quammen suggests, even a necessary one to maintain a natural diversity. He refers to it as the "yang" to the "yin" of the origin of new species.

This equilibrium can be unbalanced by several factors, however, including human activity. The fragmentation of mainland ecosystems into smaller areas can create extinctions faster than new species can arise to replace the ones that are lost. The introduction of invasive species can cause a cascading effect as they alter the food chain or environment, upsetting the balance.

It is this upsetting of the equilibrium that is the most harmful, Quammen suggests, not simply extinction itself, which is a naturally occurring part of evolution.



Style

Perspective

Quammen's larger subject is the natural environment and the changes it is undergoing presently and he approaches it as someone with a great appreciation for the diversity of nature and concern about the potential for losing that diversity. He stops short of drawing many conclusions himself, however, instead positioning himself as an interpreter of the prevailing scientific thinking on the subject of biogeography as well as the history of the development of the field.

In this role, Quammen frequently assumes the perspective of his own readers as he imagines them processing the information he is presenting. He presents the outline of a major line of thinking, but draws back before delving into the deeper scientific aspects, apologizing to his reader directly for moving into dry scientific terminology. This perspective is apparently meant to display sympathy with the reader who Quammen assumes is more interested in the more entertaining details of his travels and in the personalities of the scientists and theorists he profiles.

Quammen seems to view himself as something of a naturalist and rough traveler, and appears embarrassed when he has to assume the role of a tourist, such as when he lines up to watch the feeding of the Komodo dragons or when he takes a pleasure boat to the remote island of Aru. His disdain for the "extravagant convenience" of the pleasure boat to Aru is evident (p. 616), and he seems genuinely pleased that his own cabin is the smallest and least comfortable. He loathes the "white people with money belts and cameras" who share the boat with him. (pg. 615.)

Quammen does not pretend to offer an objective view of his subject, but he does strive to counterbalance the current competing theories about how best to address the matter of diminishing natural habitat. Ultimately, his perspective is hopeful, both that science will come to a consensus on the best path forward and that nature will find a way to survive.

Tone

Quammen strives to maintain a casual tone throughout his book. He frequently includes idiomatic constructions and conversational language, often addressing the reader directly.

Quammen carefully avoids providing too much intricate detail regarding the often complex theories under discussion, apologizing directly to the reader for getting bogged down in dry scientific description. This deliberate avoidance of the finer details produces a tone that at times seems hostile to the subject. Quammen seems to have a dislike for mathematics, for example, and assumes his readers do as well. In Chapter V, for example, after giving a brief synopsis of Frank Preston's mathematical analysis of



species distribution, Quammen writes, "Hello, are you still with me? Have you forgiven me for mentioning logarithms?" (pg. 392.)

Quammen also interjects a personal tone into his writing, especially in the sections that are more like a travelogue than scientific explanation. He describes many short episodes during his travels while researching the book that have little to do with his central subject. The story of his mugging in Rio de Janeiro in Chapter IX, for example, is purely incidental, as is his description of his fellow passengers on a boat trip to the island of Aru in the final chapter. When recounting his interviews with scientists, Quammen invariably includes personal details about them which sometimes approach the level of plain gossip.

Pervading both the scientific and personal sections of the book is a consistent tone of irreverence, punctuated by Quammen's frequent use of profanity and slight humor.

Structure

Quammen divides the book into ten chapters arranged loosely by subject. Over the course of the ten chapters, he further divides the book into 178 sequentially-numbered sections. The book contains several maps interspersed in the text, a glossary, bibliography, endnotes, and an index.

The first chapter, entitled "Thirty-Six Persian Throw Rugs" is a brief introduction to the basic premise of the text, which is that the world's ecosystems are being fragmented in ways that create virtual islands of habitat. Chapter II is called "The Man Who Knew Islands," referring to Alfred Wallace, the 19th-century naturalist who co-discovered the process of natural selection around the same time as Charles Darwin. Chapter III, "So Huge a Bignes," is named after an early sailor's description of the enormous Galapagos tortoise, and examines some of the observed tendencies of island-dwelling species to tend toward extremes in size.

"Rarity Unto Death" is the title of Chapter IV, which introduces the idea of a population of a species dwindling to a point where it has little chance of remaining sustainable. Chapter V is called "Preston's Bell" after the observation made by the scientist Frank Preston that plotting species by their commonness and rarity produces a bell-shaped curve. "The Coming Thing," Chapter VI, further examines the impact of a well-known book called "The Theory of Island Biogeography."

Chapter VII is entitled "The Hedgehog of the Amazon," in reference to the highlyfocused ecologist Tom Lovejoy, who is profiled in this chapter. Chapter VIII is called "The Song of the Indri" and is about a rare species of lemur living in Madagascar. "World in Pieces," Chapter IX, is a summary chapter that brings the ideas of island biogeography to a mainland setting. The final chapter is called "Message from Aru" and provides a hopeful epilogue to the book as the author visits one of the places originally described by Alfred Wallace.



Quotes

"For the past thirty years, professional ecologists have been murmuring about the phenomenon of unraveling ecosystems. Many of these scientists have become mesmerized by the phenomenon and, increasingly with time, worried" (Chapter I, pg. 11.)

"Biogeography is the study of the facts and the patterns of species distribution. It's the science concerned with where animals are, where plants are, and where they are not" (Chapter II, pg. 17.)

"Old versus young is just one crucial dichotomy that affects the biological richness of an island. Small versus large is another. Continental versus oceanic, in the sense that biogeographers use the terms, is a third" (Chapter II, pg. 52.)

"The patterns of species distribution have provided clues about the ways in which species originate, change and diverge, and the question how? has remained inseparable from the question where?" (Chapter III, pg. 117.)

"We notice a commotion just ahead in the brush. Then a very large komodo breaks into view, spooked by our trespass, and scrambles straight up the vertical face of the bluff, like an alligator scaling a four-story building. Lumps of rock crumble and fall. My jaw drops like the lid of a dumpster" (Chapter III, pg. 172.)

"The extinction of the dodo is representative of modernity in several different ways, not least of which is that the event occurred on a small island" (Chapter IV, pg. 263.)

"Why is rarity perilous? Why do small populations go extinct? The answer is simple in outline and complicated in its scientific details. For now, let's stick with the outline version" (Chapter IV, pg. 293.)

"The species-area relationship is one of ecology's oldest and most profound generalizations. Exactly how old and exactly how profound are matters still under discussion" (Chapter V, pg. 385.)

"MacArthur felt that the science of ecosystems should venture beyond description. It shouldn't limit itself to collecting and indexing facts. It should find broader patterns in the natural world, and from those patterns it should extract general principles" (Chapter VI, pg. 410.)

"The equilibrium theory of island biogeography is not a piece of conceptual art. It's a tool. MacArthur and Wilson developed it for two reasons: to explain and to predict" (Chapter VI, pg. 420.)

"The lesson of these early data was unmistakable. A tiny patch of Amazon rainforest one hectare, say, or even ten - could not maintain its existence in isolation. It just wasn't big enough to sustain itself" (Chapter VII, pg. 472.)



"In the late 1970s, a few ecologists began using a pregnant new term: minimum viable population" (Chapter VIII, pg. 512.)

"Most of these cops are jaunty young plainclothes men in colorful sport shirts and pastel pants who have evidently imprinted their professional self-image from reruns of Miami Vice" (Chapter IX, pg. 581.)

"Like most dugout canoes, this one is shallow and light, with almost no freeboard - carefully crafted so as to be astonishingly uncomfortable and unstable for people with stiff joints and pale skin" (Chapter X, pg. 624.)



Topics for Discussion

What role does extinction play in the balance of nature?

How does Quammen approach the various scientific debates he writes about? Does he take sides?

Quammen frequently uses sarcasm in his writing. To what degree is this effective?

What kind of book is "The Song of the Dodo?" Is it a science book, travelogue, or autobiography? Does it succeed?

Is the controversy over how Darwin treated Wallace important to Quammen's thesis? Why does he include it?

Does Quammen reach any solid conclusions or suggest any solutions to the questions he asks?

Quammen's book is divided into dozens of very short sections. Is this an effective arrangement? Why or why not?