Determinants of Extinction

Paleobiology

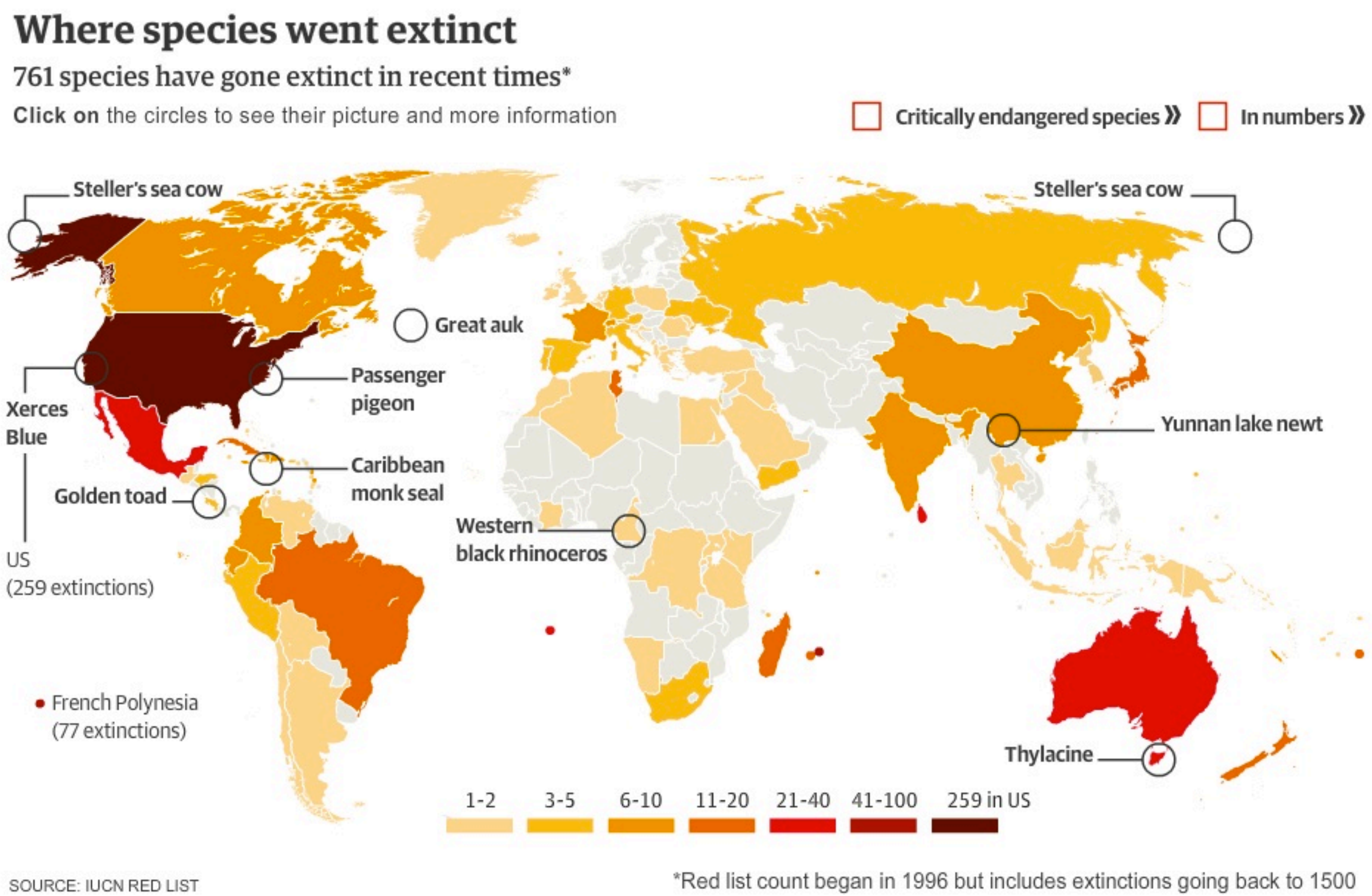
February 15, 2016

Extinction is really easy

- David M. Raup
  - Most people that have ever lived are alive today.
  - Most computer scientists and nuclear physicists are alive today.

- Most species are not, the current estimate is that 99.9% of all species that have ever lived are extinct.

Extinction is really easy



Many modern extinctions are not

biology letters
Biol. Lett. (2007) 3, 581–584
doi:10.1098/rsbl.2007.0316
Published online 31 July 2007
Population ecology

Short-term climate change and the extinction of the snail *Rhachistia aldabrae* (Gastropoda: Pulmonata)

Justin Gerlach*

Nature Protection Trust of Seychelles, 133 Cherry Hinton Road, Cambridge CB1 7BX, UK
**jstgerlach@aol.com*

The only known population of the Aldabra banded snail *Rhachistia aldabrae* declined through the late twentieth century, leading to its extinction in the late 1990s. This occurred within a stable habitat and its extinction is attributable to decreasing rainfall on Aldabra atoll, associated with regional changes in rainfall patterns in the late twentieth and early twenty-first century. It is proposed that the extinction of this species is a direct result of decreasing rainfall leading to increased mortality of juvenile snails.

Keywords: Mollusca; extinction; Aldabra atoll; rainfall

The rediscovery of the Aldabra banded snail, *Rhachistia aldabrae*

Richard W. Battarbee

Editor-in-Chief

RWB, 0000-0003-3963-6228

In 2007, we published an article by Justin Gerlach reporting that the population of the Aldabra banded snail, *Rhachistia aldabrae*, had declined during the latter part of the twentieth century and had become extinct in the late 1990s [1]. This conclusion was based on the analysis of data from a range of shell collections made across the different islands of the Aldabra atoll from 1895 through to 2006. Gerlach noted that no juveniles had been collected since 1976, and no live adults since 1996, despite systematic surveys aimed specifically at finding the snail in 2005 and 2006. After examining the data, Gerlach discounted changes in habitat, predator pressure or diet as reasons for the population change. He argued, on the basis of a correlation between snail numbers and rainfall, that its decline and proposed extinction was due to a change in climate, namely decreased rainfall, claiming that juveniles were unable to tolerate extended dry periods.

Many modern extinctions are not

biology letters

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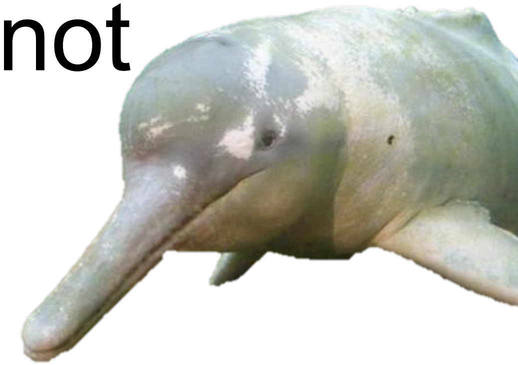
Marine biology

First human-caused extinction of a cetacean species?

Samuel T. Turvey[1], Robert L. Pitman[2], Barbara L. Taylor[2], Jay Barlow[2], Tomonari Akamatsu[3], Leigh A. Barrett[4], Xiujiang Zhao[5,6], Randall R. Reeves[7], Brent S. Stewart[8], Kexiong Wang[5], Zhuo Wei[5], Xianfeng Zhang[5], L. T. Pusser[9], Michael Richlen[10], John R. Brandon[11] and Ding Wang[5,*]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*
[2]*NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, CA 92037, USA*
[3]*NRIFE, Fisheries Research Agency, Hasaki, Kamisu, Ibaraki 314-0408, Japan*
[4]*Baiji.org Foundation, Klosbachstrasse 106, 8032 Zurich, Switzerland*
[5]*Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*
[6]*Chinese Academy of Sciences Graduate School, Beijing 100039, China*
[7]*Okapi Wildlife Associates, Hudson, Quebec, Canada J0P 1H0*
[8]*Hubbs-SeaWorld Research Institute, 2595 Ingraham Street, San Diego, CA 92109, USA*
[9]*PO Box 122, West End, NC 27376, USA*
[10]*Department of Zoology, University of Hawai'i, Edmondson 152, Honolulu, HI 96822, USA*
[11]*University of Washington, School of Aquatic and Fisheries Sciences, Box 355020, Seattle, WA 98195, USA*
**Author for correspondence (wangd@ihb.ac.cn).*



Extinction means everyone

Historical DNA analysis reveals living descendants of an extinct species of Galápagos tortoise

Nikos Poulakakis*†‡, Scott Glaberman*†, Michael Russello*†§, Luciano B. Beheregaray¶, Claudio Ciofi‖, Jeffrey R. Powell*, and Adalgisa Caccone*

*Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520; §Unit of Biology and Physical Geography, University of British Columbia Okanagan, Kelowna, BC, Canada V1V 1V7; ¶Department of Biological Sciences, Macquarie University, Sydney NSW 2190, Australia; and ‖Department of Evolutionary Biology, University of Florence, 50125 Florence, Italy

Edited by David B. Wake, University of California, Berkeley, CA, and approved July 30, 2008 (received for review June 4, 2008)

Giant tortoises, a prominent symbol of the Galápagos archipelago, illustrate the influence of geological history and natural selection on the diversification of organisms. Because of heavy human exploitation, 4 of the 15 known species (*Geochelone* spp.) have disappeared. Charles Darwin himself detailed the intense harvesting of one species, *G. elephantopus*, which once was endemic to the island of Floreana. This species was believed to have been exterminated within 15 years of Darwin's historic visit to the Galápagos in 1835. The application of modern DNA techniques to museum specimens combined with long-term study of a system creates new opportunities for identifying the living remnants of extinct taxa in the wild. Here, we use mitochondrial DNA and microsatellite data obtained from museum specimens to show that the population on Floreana was evolutionarily distinct from all other Galápagos tortoise populations. It was demonstrated that some living individuals on the nearby island of Isabela are genetically distinct from the rest of the island's inhabitants. Surprisingly, we found that these "non-native" tortoises from Isabela are of recent Floreana ancestry and closely match the genetic data provided by the museum specimens. Thus, we show that the genetic line of *G. elephantopus* has not been completely extinguished and still exists in an intermixed population on Isabela. With enough individuals to commence a serious captive breeding program, this finding may help reestablish a species that was thought to have gone extinct more than a century ago and illustrates the power of long-term genetic analysis and the critical role of museum specimens in conservation biology.

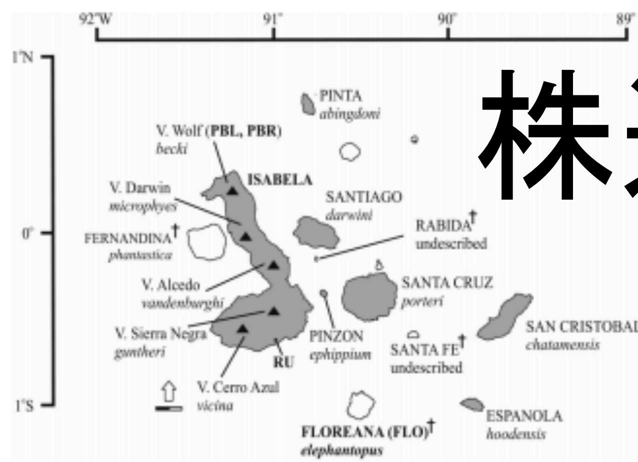


Fig. 1. Distribution of giant tortoises in the Galápagos archipelago. Shaded and non-shaded islands indicate presence of extant and extinct tortoise populations, respectively. Italicized names indicate current taxonomic designations (5, 8). Pinta is represented by a single male kept in captivity. †: extinct species. ▲: volcanoes on Isabela.

株連九族

The taxonomic ranking of populations on different islands and volcanoes, often morphologically distinct, has been con-

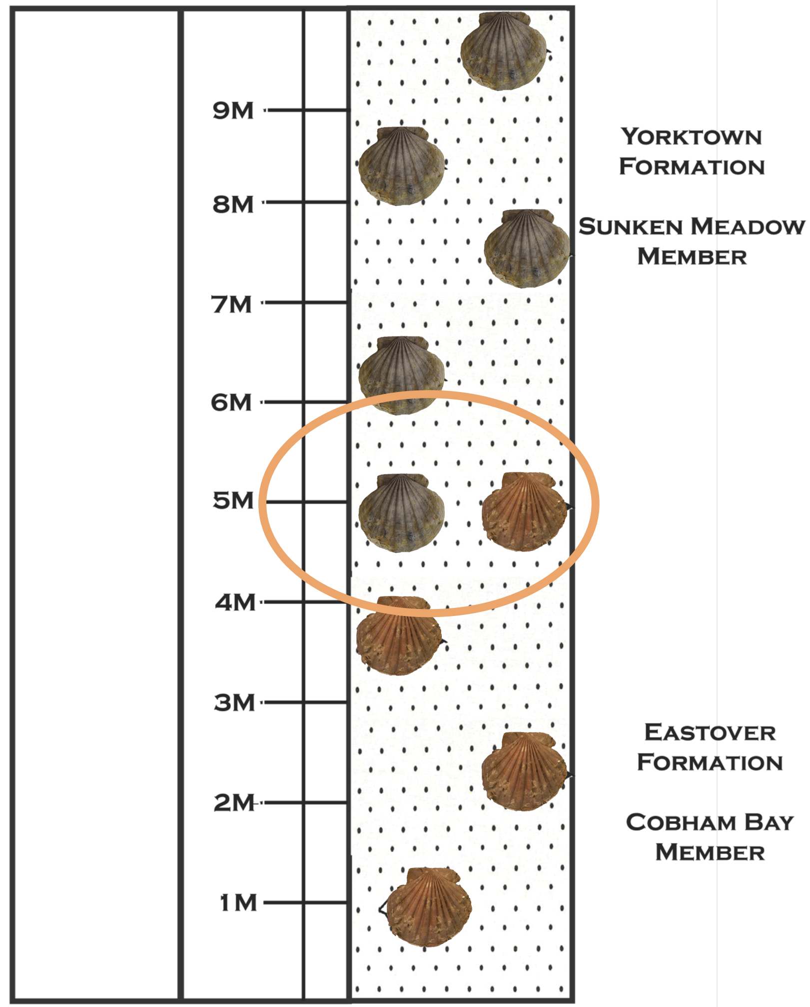
What is extinction?

brakken.tumblr.com

- Anagenesis – rapid evolution of a daughter from a parent, such that no populations of parent and daughter are contemporary.
- Cladogenesis – The parent and daughter species coexist for a period of time.

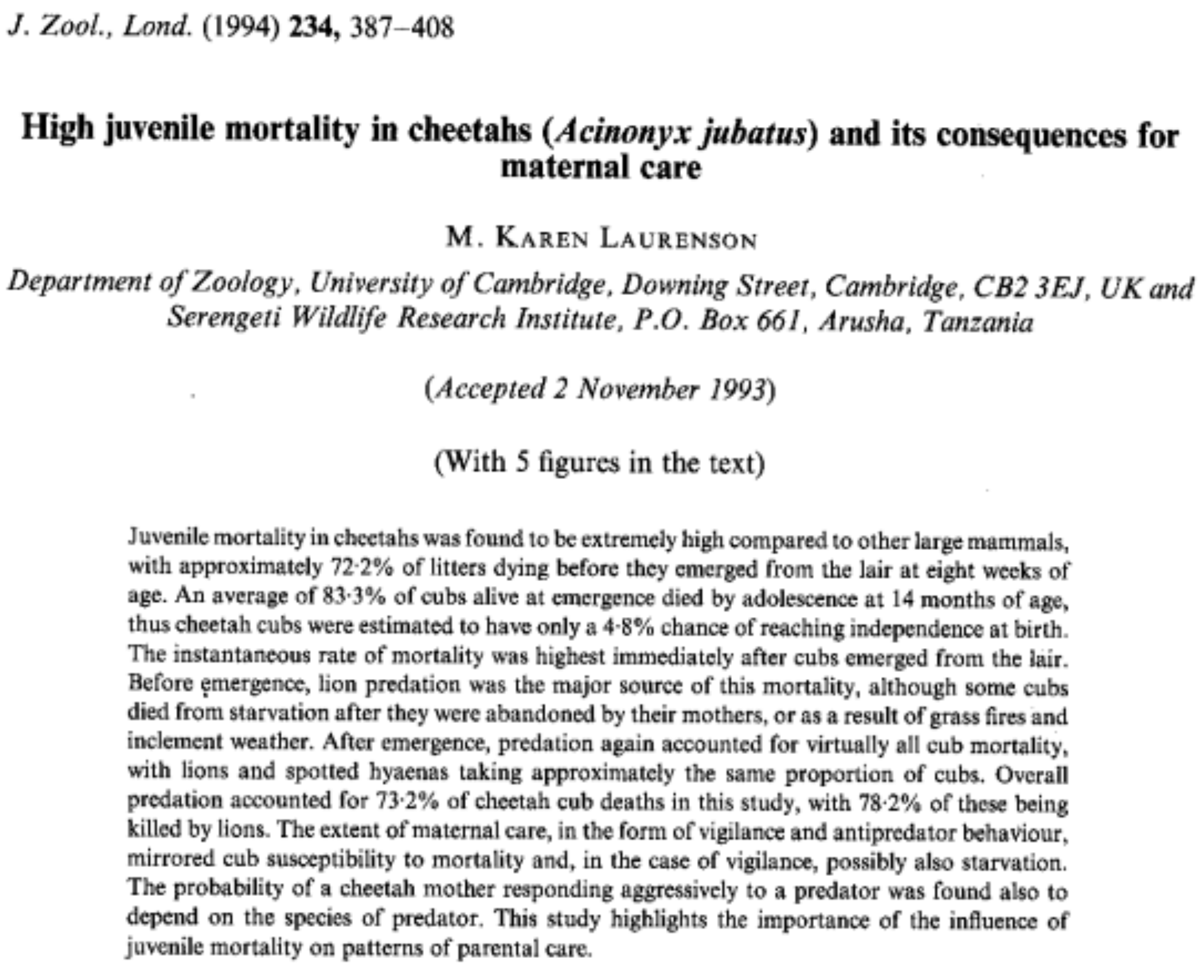
How can we tell?

How can we tell?



Cope's Law (not rule)

- Evolutionary Trap



J. Zool., Lond. (1994) **234,** 387–408

High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care

M. KAREN LAURENSON

Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK and Serengeti Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania

(*Accepted 2 November 1993*)

(With 5 figures in the text)

Juvenile mortality in cheetahs was found to be extremely high compared to other large mammals, with approximately 72·2% of litters dying before they emerged from the lair at eight weeks of age. An average of 83·3% of cubs alive at emergence died by adolescence at 14 months of age, thus cheetah cubs were estimated to have only a 4·8% chance of reaching independence at birth. The instantaneous rate of mortality was highest immediately after cubs emerged from the lair. Before emergence, lion predation was the major source of this mortality, although some cubs died from starvation after they were abandoned by their mothers, or as a result of grass fires and inclement weather. After emergence, predation again accounted for virtually all cub mortality, with lions and spotted hyaenas taking approximately the same proportion of cubs. Overall predation accounted for 73·2% of cheetah cub deaths in this study, with 78·2% of these being killed by lions. The extent of maternal care, in the form of vigilance and antipredator behaviour, mirrored cub susceptibility to mortality and, in the case of vigilance, possibly also starvation. The probability of a cheetah mother responding aggressively to a predator was found also to depend on the species of predator. This study highlights the importance of the influence of juvenile mortality on patterns of parental care.

Cope's Law (not rule)

- Does (morphological) specialization affect extinction?

A Test of Simpson's "Rule of the Survival of the Relatively Unspecialized" Using Fossil Crinoids

Lee Hsiang Liow*

Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637

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Online enhancements: appendixes, tables, figures.

ABSTRACT: Temporally long-ranging (=long-lived) taxa have been postulated to have unusual properties that aid their prolonged geologic survival. Past studies have examined dispersal capabilities, geographic ranges, and single-character morphological adaptations as factors that may contribute to geologic longevity. Here, I test whether long-lived fossil crinoid taxa are morphologically unusual using a whole suite of morphological characters. I define long-lived taxa in several explicit, comparative ways. I find that long-lived crinoid genera and families are often less distant from mean morphologies of their crinoid orders than their shorter-lived relatives; that is, they are relatively less specialized. I also compare the morphology of crinoid genera relative to basal members of their respective orders; mean morphological distances of long-lived genera from basal morphologies are seldom distinct from those of their shorter-lived relatives. I observe that long-lived crinoid genera are less distant from mean morphologies of their temporal cohorts compared with shorter-lived genera but not in a statistically significant manner. I conclude that long-lived crinoids are relatively unspecialized, in the sense that they are relatively closer to mean morphologies of their taxonomic groups.

Keywords: long-lived taxa, persistence, morphology, fossil.

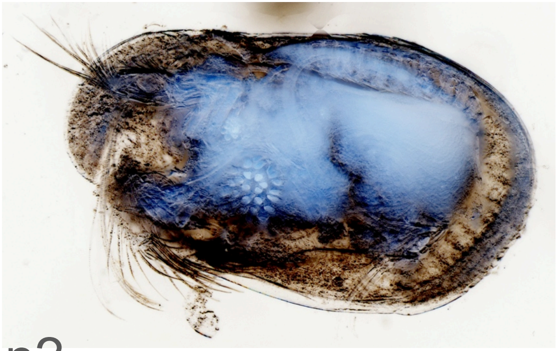
Eldredge and Stanley (1984), and Avise et al. (1994) have discussed "living fossils" and the related phenomena of arrested evolution, bradytely, and morphological stasis or conservatism.

Long-lived taxa are commonly thought to survive longer than related shorter-lived taxa because they are unique, unusual, or exceptional in some significant way. They allegedly reside in unusual habitats (Selander et al. 1970; Parsons 1994) or have distinctive morphological features not shared by shorter-lived taxa (Ward and Signor 1983; Kammer et al. 1998). Many previous studies on "living fossils" have characterized them as paradoxical, relictual, primitive, or special (e.g., McKenzie 1967; Mooi 1990; King and Hanner 1998; Eisner 2003) without exploring the phenomenon of longevity in a comparative and quantitative manner. Here, I use a quantitative approach to examine whole clades in order to discover any shared patterns among long-lived taxa. I use three explicit definitions of "long lived" (see "Data Treatment"). Long-lived taxa defined as such are not necessarily designated by other authors as "living fossils."

Crinoids (feather stars and sea lilies) belong to the exclusively marine phylum Echinodermata. Crinoids have been chosen as an illustrative taxon for several reasons. First, crinoids are monophyletic (Janies 2001). Second, they are morphologically conservative enough to allow meaningful comparative analysis. Third, they are diverse enough to provide large samples for quantitative study.

- Morphologically "simpler" crinoids do live longer than more morphologically "deviant" crinoids.
- Simpson's Rule = Cope's Law

Cope’s Law (not rule)



- Does (morphological) specialization affect extinction?

Paleobiology, 32(1), 2006, pp. 55–69

Do deviants live longer? Morphology and longevity in trachyleberidid ostracodes

Lee Hsiang Liow

Abstract.—Persistent fossil taxa contravene paradigms of evolution: pervasive morphological change and taxic turnover. Comparative studies of taxic duration have often been approached from biogeographic, climatic, and ecological perspectives, with a focus on process. Here I use a morphological approach to study the pattern of longevity of a large family of marine living and fossil podocopid ostracodes, Trachyleberididae sensu lato. I test if geologically longer-lived genera are collectively morphologically more deviant from a group mean than their shorter-lived relatives by using both discrete morphological data and outline data. I discovered that long-lived genera are in general not significantly more or less morphologically deviant from the average morphology than their shorter-lived relatives. However, I found that contemporaneous subsets of long-lived trachyleberidids are often at least marginally significantly more deviant in discrete morphology than shorter-lived ones, especially in external morphology. No significant patterns of association between morphological deviation and durations in other subdivisions of the data emerged (i.e., whole data set, birth cohorts, groups of morphological characters, and outline data using both Fourier analysis and eigenshape analysis). This is in contrast to a previous finding that long-lived genera of crinoids within orders are often morphologically less deviant than their shorter-lived relatives than expected by chance.

Lee Hsiang Liow *Committee on Evolutionary Biology, University of Chicago, 5734 South Ellis Avenue, Hinds 269, Chicago, Illinois 60637. E-mail: lhliow@midway.uchicago.edu*

Accepted: 11 May 2005

- Morphologically “simpler” ostracodes do not live longer than more morphologically “deviant” ostracodes.
- Simpson’s Rule = Cope’s Law

Cope's Rule and Body Size

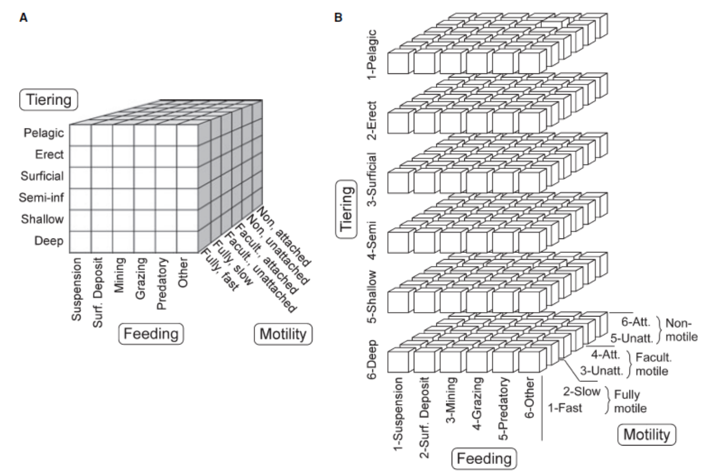
- The general hypothesis is that larger (body) sized organisms are more vulnerable to extinction than smaller (body) sized organisms.
  - Sometimes hypothesized at the intra-clade level.
  - Sometimes hypothesized and the inter-clade level.
- There are many documented cases where this is demonstrably false.
  - Most cases supporting a body size and extinction relationship come from terrestrial vertebrates.
  - In cases where body size is related to extinction, it is difficult to separate out whether or not this is because body size is related to some other, more fundamental, factor.

Selecting against bad habits

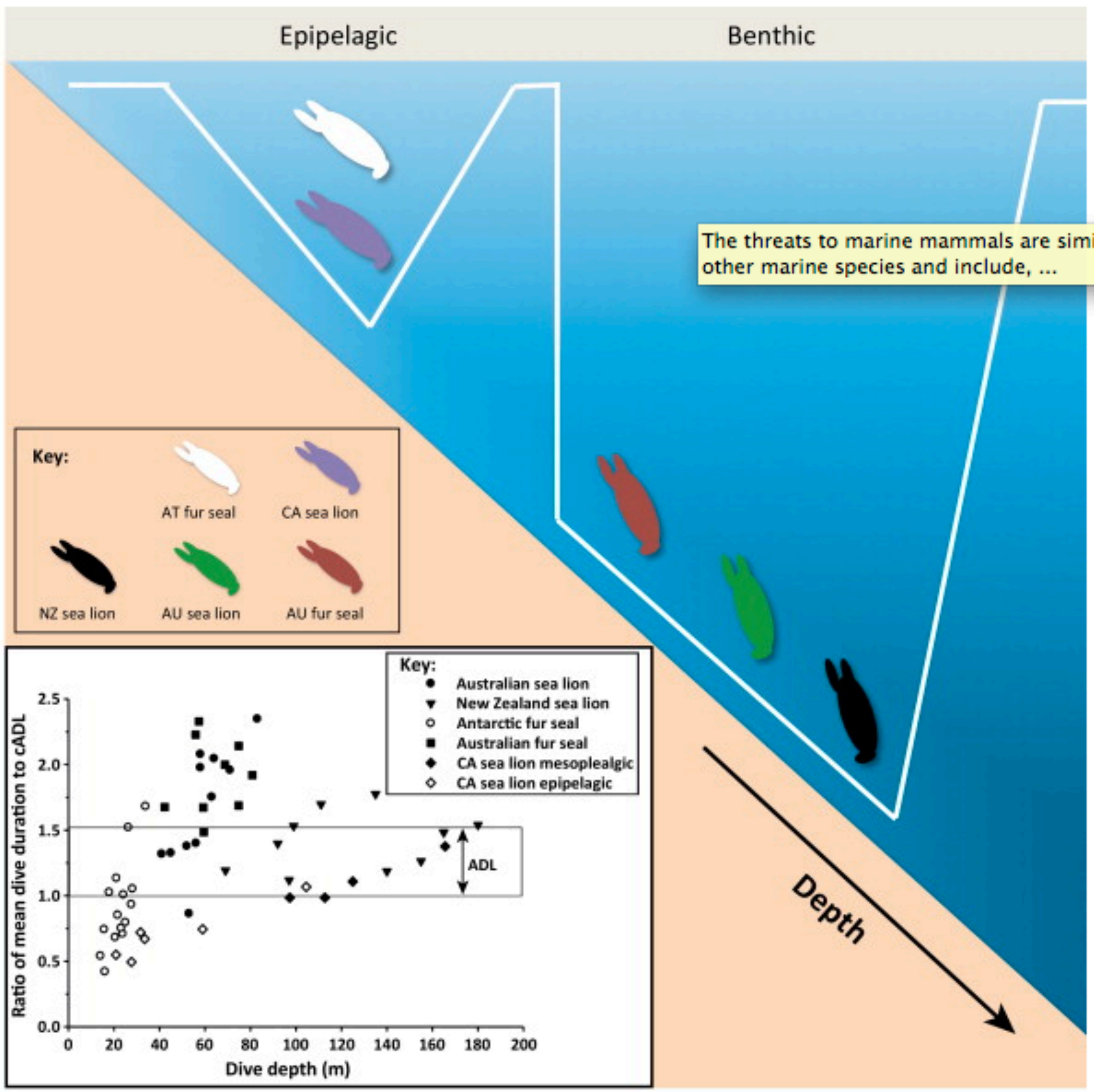
Selectivity of End-Cretaceous Marine Bivalve Extinctions

David Jablonski* and David M. Raup

Analyses of the end-Cretaceous or Cretaceous-Tertiary mass extinction show no selectivity of marine bivalve genera by life position (burrowing versus exposed), body size, bathymetric position on the continental shelf, or relative breadth of bathymetric range. Deposit-feeders as a group have significantly lower extinction intensities than suspension-feeders, but this pattern is due entirely to low extinction in two groups (Nuculoida and Lucinoidea), which suggests that survivorship was not simply linked to feeding mode. Geographically widespread genera have significantly lower extinction intensities than narrowly distributed genera. These results corroborate earlier work suggesting that some biotic factors that enhance survivorship during times of lesser extinction intensities are ineffectual during mass extinctions.

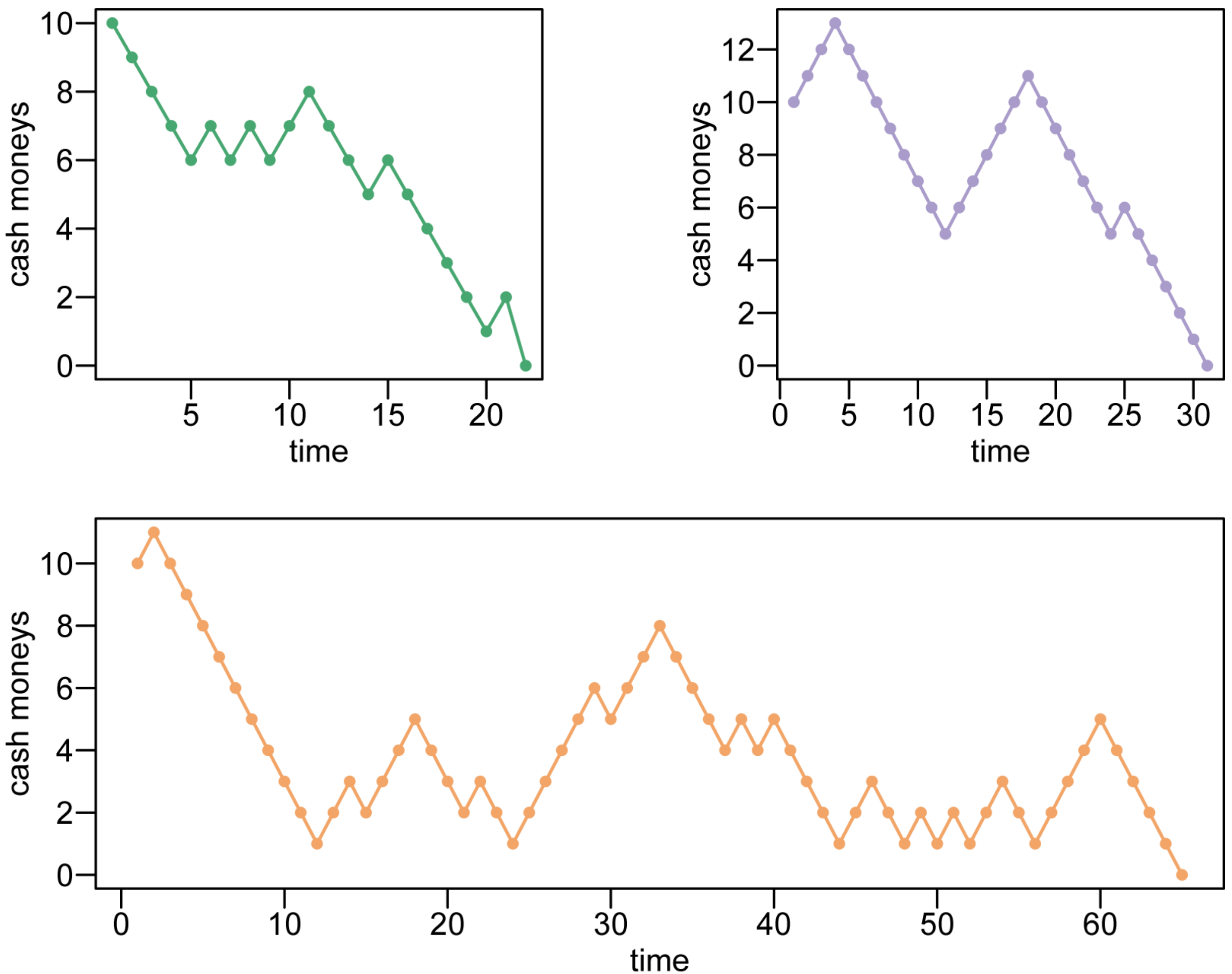


Organism specific

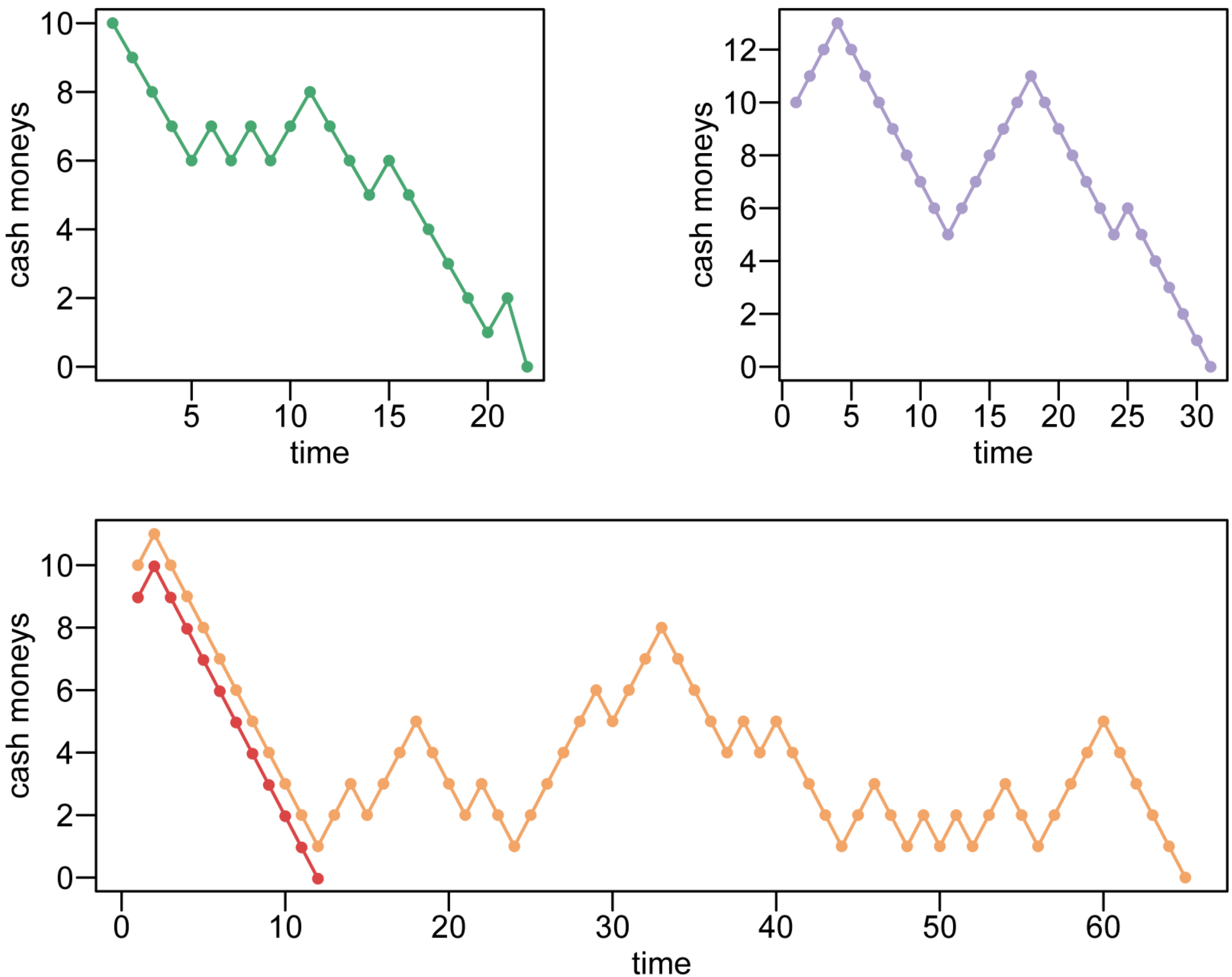


- Part of this course's philosophy is that we are looking for *general* factors that can apply in many time-periods and to many taxa.
- However, this does not mean that specific or unique conditions are unimportant, and we should endeavour to remember them.

Gambler's ruin



Gambler’s ruin



Random walks teach us…

- The larger your abundance the further away you are from extinction, the likelier you are to live… in a fair world.

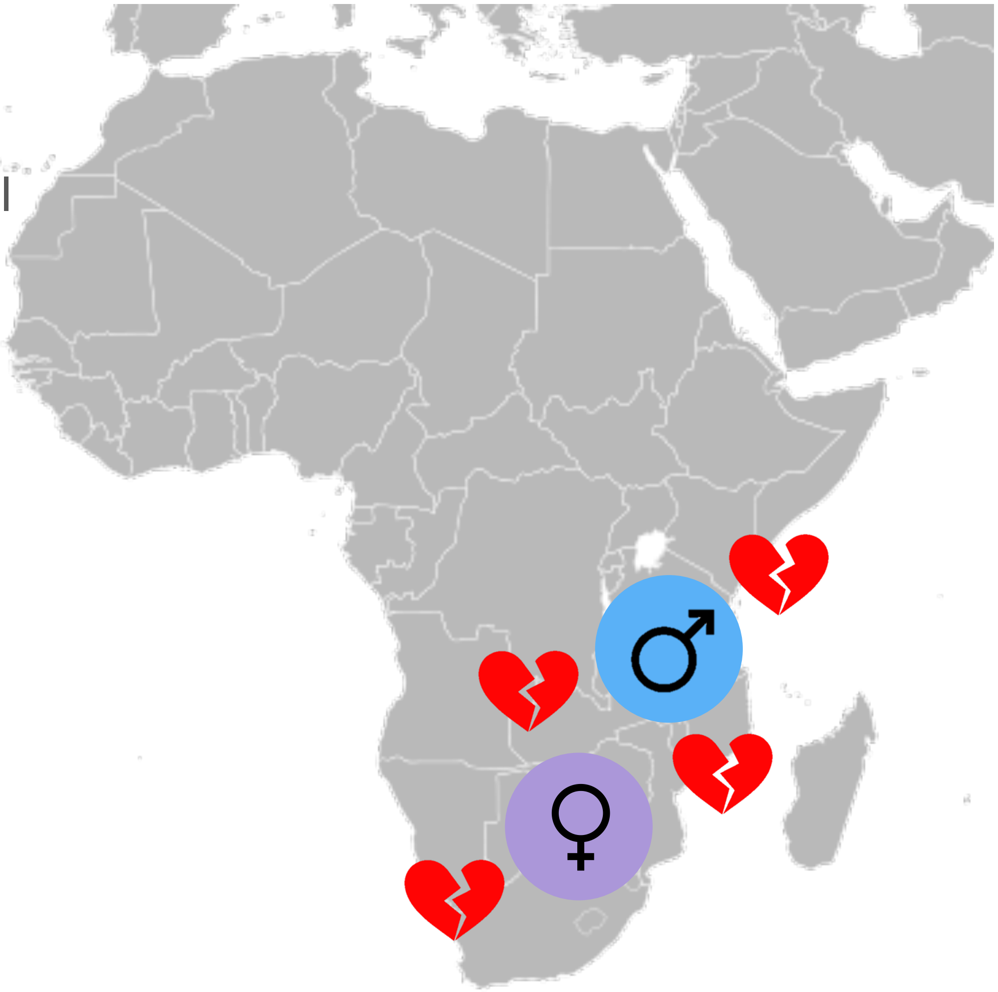
- Huygen’s Theorem – in a fair game of infinite length, you will eventually reach extinction.

- We can model lots of ecological variables as random walks, particularly those with a zero lower bound.
  - Population Size/Abundance
  - Geographic Range Size
  - Body Size

- You can easily simulate a random walk in R using the `cumsum( )` and `sample( )` functions.
  - `cumsum(sample(c(-1,1), n, replace=TRUE))`, where n is the duration of the walk.

Allee effect

- Warner Clyde Allee
  - Density Dependence
    - Population size can change behavioral, physical, or statistical properties of species



- Mate limitation
  - A population size feedback loop.

Is abundance related to extinction?

Paleobiology, 38(2), 2012, pp. 278–291

Abundance and extinction in Ordovician–Silurian brachiopods, Cincinnati Arch, Ohio and Kentucky

Andrew Zaffos and Steven M. Holland

Abstract.—A basic hypothesis in extinction theory predicts that more abundant taxa have an evolutionary advantage over less abundant taxa, which should manifest as increased survivorship during major extinction events and longer fossil-record durations. Despite this, various paleontologic studies have found conflicting patterns, indicating a more complex relationship between abundance and extinction in the geologic past. This study tests the relationship between abundance and extinction among brachiopod genera within seven third-order depositional sequences spanning the Late Ordovician to Early Silurian (Katian–Aeronian) of the Cincinnati Arch.

Contrary to predictions, abundance is not positively correlated with duration in this study. Abundance and duration range from strongly negatively correlated to uncorrelated depending on the spatial scale of analysis and the geologic intervals included, but correlations never indicate that abundance is an evolutionary advantage. In contrast, abundance was an advantageous trait prior to the Ordovician/Silurian extinction, and brachiopods with higher abundances were more likely to survive the event than less abundant brachiopods. While this result is in keeping with common models of extinction, it has not been observed previously at a mass extinction boundary. This may be further evidence that the Ordovician/Silurian extinction was not accompanied by a shift in the macroevolutionary selectivity regime.

Andrew Zaffos and Steven M. Holland. Department of Geology, The University of Georgia, Athens, Georgia 30602-2501. E-mail: zaffosaa@mail.uc.edu

- Some have found positive, negative, or neutral relationships.
- Very few studies in the fossil record show a relationship between abundance/population size and extinction risk.

Is abundance related to extinction?

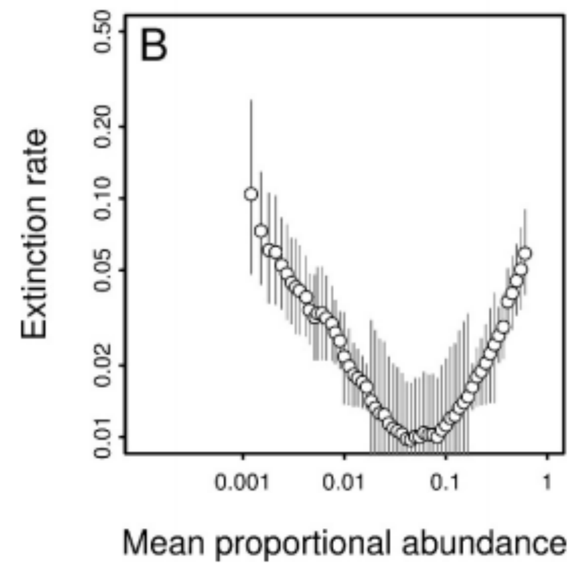
Paleobiology, 35(4), 2009, pp. 631–647

Assessing the role of abundance in marine bivalve extinction over the post-Paleozoic

Carl Simpson and Paul G. Harnik

Abstract.—Abundance is one of the primary factors believed to influence extinction yet little is known about its relationship to extinction rates over geologic time. Using data from the Paleobiology Database we show that abundance was an important factor in the extinction dynamics of marine bivalve genera over the post-Paleozoic. Contrary to expectations, our analyses reveal a nonlinear relationship between abundance and extinction rates, with rare and abundant genera exhibiting rates elevated over those of genera of moderate abundance. This U-shaped pattern is a persistent feature of the post-Paleozoic history of marine bivalves and provides one possible explanation for why we find strong support for heterogeneous extinction rates among genera grouped by similarity in abundance yet effectively no net relationship among these rates when using models of directional selection on abundance.

Carl Simpson. Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany. E-mail: Carl.Simpson@mfn-berlin.de
Paul G. Harnik. Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637. E-mail: pharnik@uchicago.edu

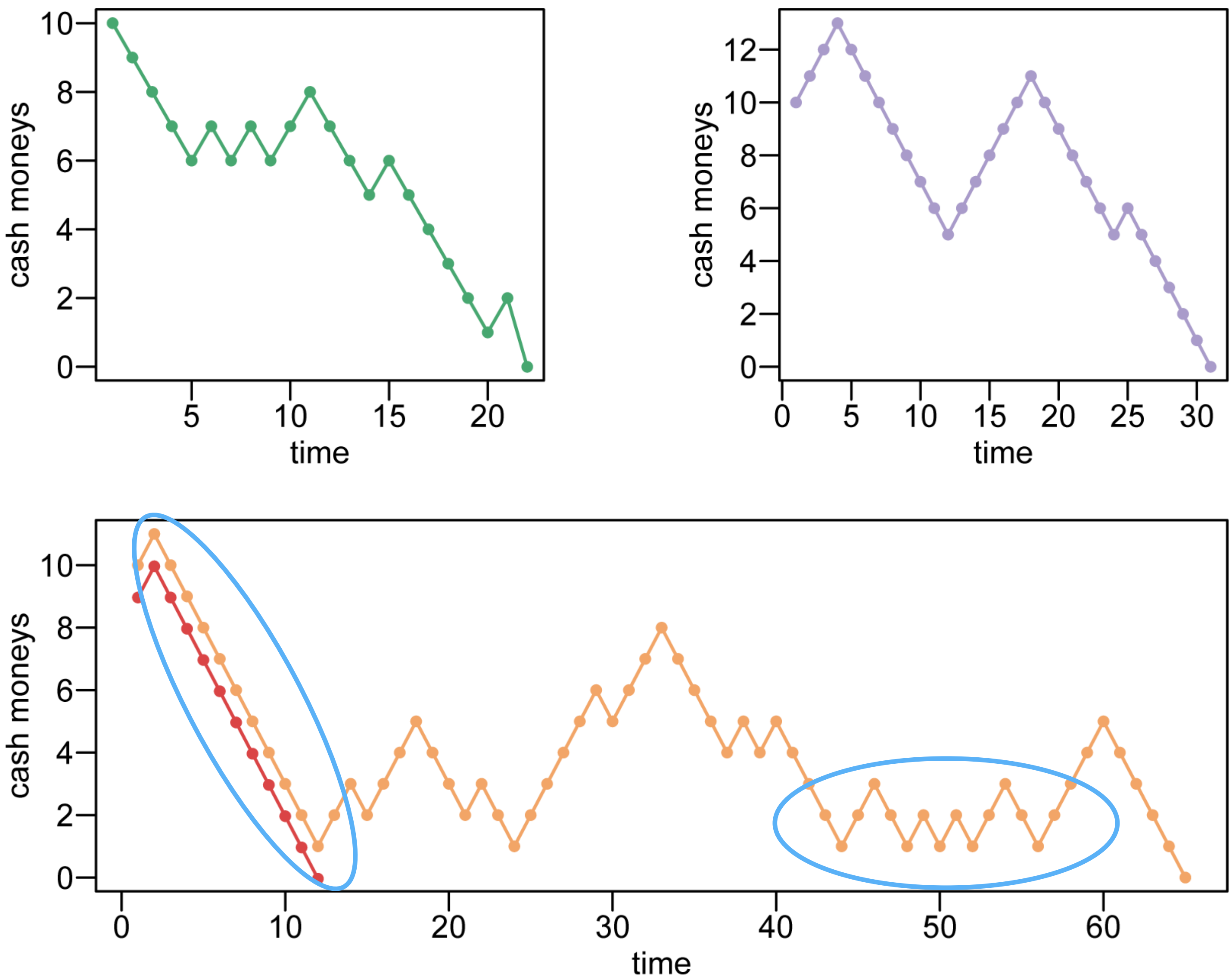


- A non-linear relationship.
- Very abundant taxa are short lived.
- Very rare taxa are short lived.

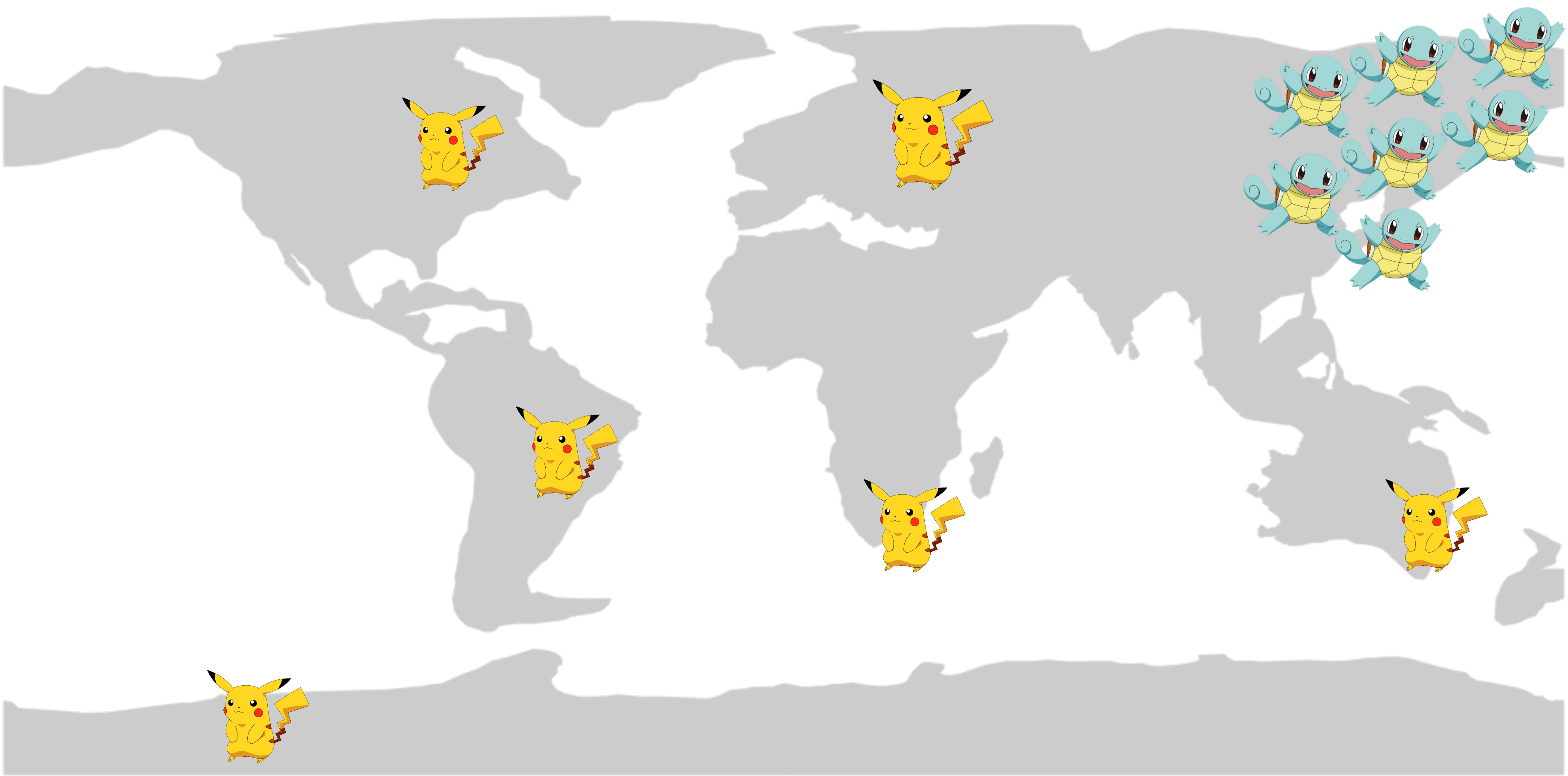
Life isn't fair

- The abundance of fossils is not the same as population size – i.e., what we are calling abundance is not abundance.
  - The current party line is that the fossil record does give a very reasonable representation of abundance.
- If random walks/gambler's ruin teach us that a fair world predicts a strong abundance and extinction relationship, then the lack of that relationship implies the world is not fair.

Rate of fall and instability



Geographic range size is king



A few considerations…

- The more widely dispersed the extinction mechanism, the less geographic range size will be a buffer against extinction.
  - Mass extinction and background extinction
  - Abundance is probably more important for extirpation than extinction.
- Abundance, Body Size, Geographic Range Size, and Specialization are all generally correlated.
  - They can, of course, also be different.
- The ecological niche determines where and when a species can exist. Niche size is not equal to geographic range size, but niches do ultimately control geographic distribution.

Geographic range size is still king

Long-term differences in extinction risk among the seven forms of rarity

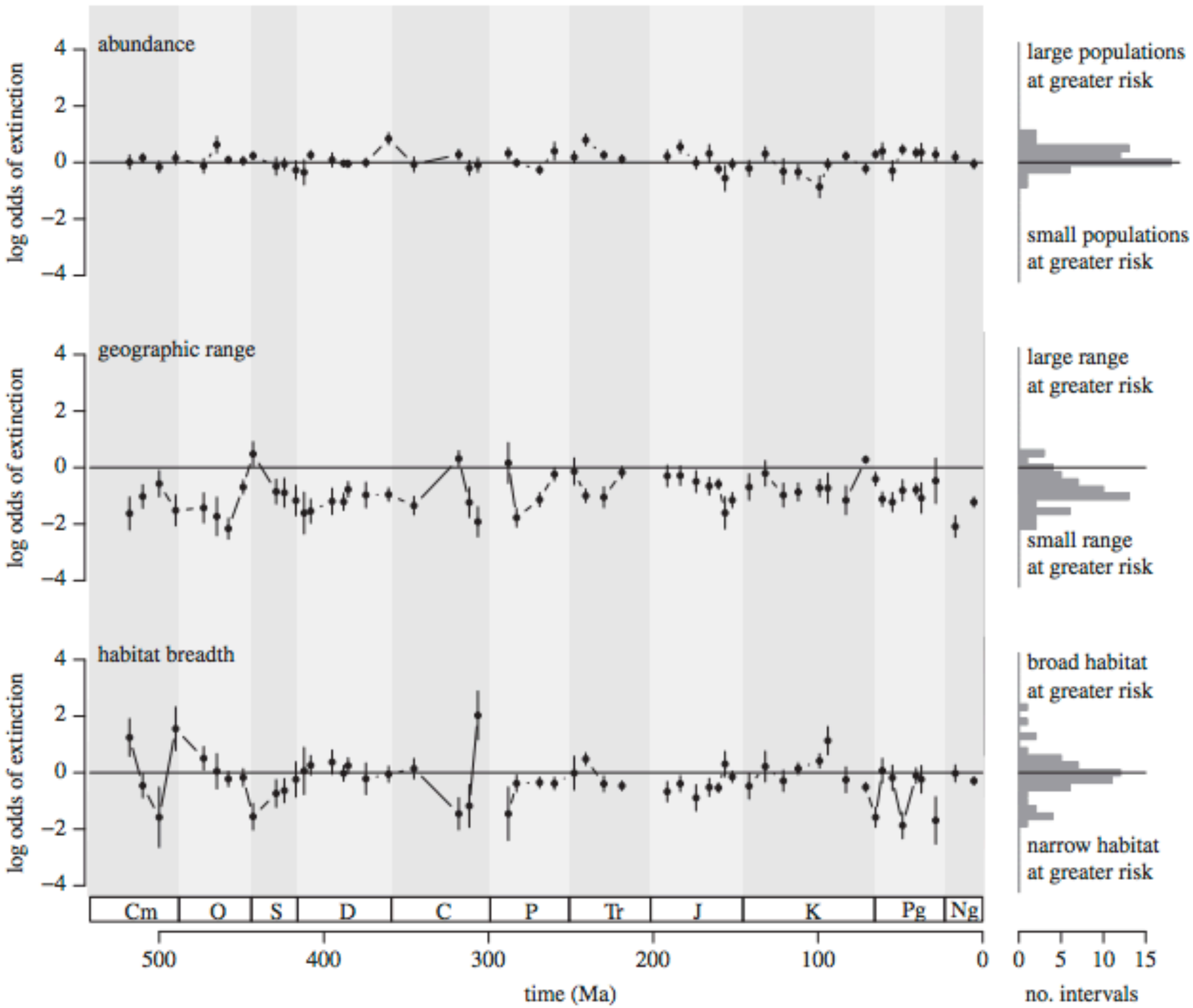
Paul G. Harnik[1,*,†], Carl Simpson[2] and Jonathan L. Payne[1]

[1] *Department of Geological and Environmental Sciences, Stanford University, Stanford, CA 94305, USA*
[2] *Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Berlin 10115, Germany*

Rarity is widely used to predict the vulnerability of species to extinction. Species can be rare in markedly different ways, but the relative impacts of these different forms of rarity on extinction risk are poorly known and cannot be determined through observations of species that are not yet extinct. The fossil record provides a valuable archive with which we can directly determine which aspects of rarity lead to the greatest risk. Previous palaeontological analyses confirm that rarity is associated with extinction risk, but the relative contributions of different types of rarity to extinction risk remain unknown because their impacts have never been examined simultaneously. Here, we analyse a global database of fossil marine animals spanning the past 500 million years, examining differential extinction with respect to multiple rarity types within each geological stage. We observe systematic differences in extinction risk over time among marine genera classified according to their rarity. Geographic range played a primary role in determining extinction, and habitat breadth a secondary role, whereas local abundance had little effect. These results suggest that current reductions in geographic range size will lead to pronounced increases in long-term extinction risk even if local populations are relatively large at present.

Keywords: Phanerozoic; invertebrate; macroevolution; macroecology; conservation

Geographic range size is still king



Clumsy segue into a discussion of odds

Hypothesis: Taxa we classify as large ranged are more likely to survive an extinction event than a smaller ranged taxon

	Large Range	Small Range	Total
Victim	227	376	603
Survivor	447	115	562
Total	674	491	1165

Clumsy segue into a discussion of odds

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$$\frac{\frac{\text{FREQUENCY TRUE}}{\text{TOTAL}}}{\frac{\text{FREQUENCY FALSE}}{\text{TOTAL}}}$$

Clumsy segue into a discussion of odds

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	Large Range	Small Range	Total
Victim	227	376	603
Survivor	447	115	562
Total	674	491	1165

$$\frac{\frac{447}{674}}{\frac{227}{674}} = 1.969$$

$$\frac{\frac{\text{FREQUENCY TRUE}}{\text{TOTAL}}}{\frac{\text{FREQUENCY FALSE}}{\text{TOTAL}}}$$

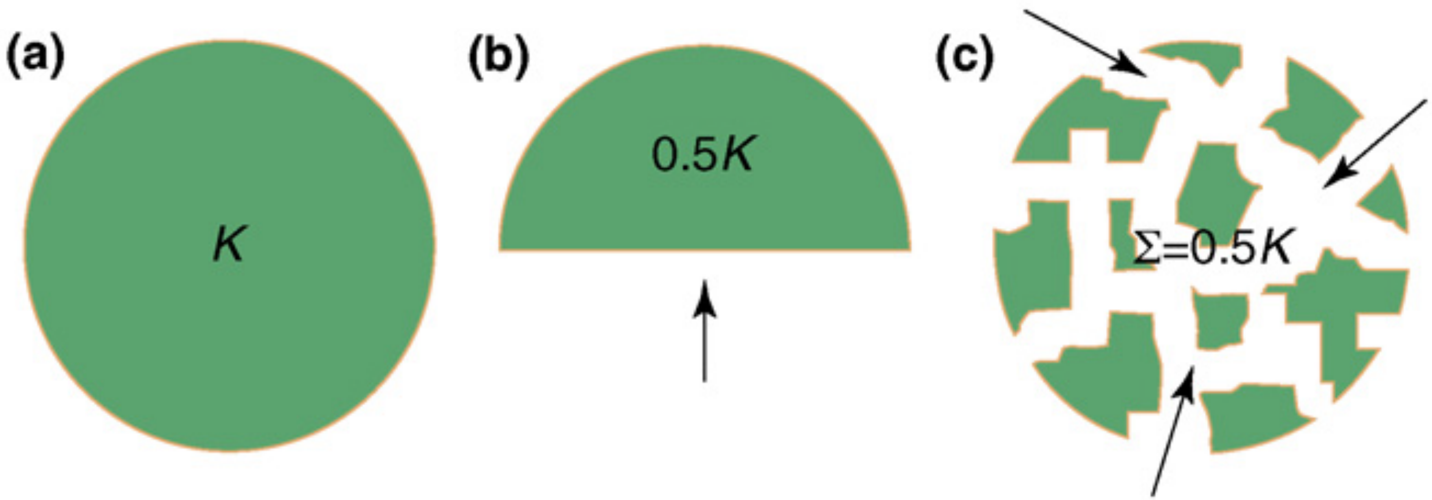
$$\frac{1.969}{0.305} = 6.455$$

$$\frac{\frac{115}{491}}{\frac{376}{491}} = 0.305$$

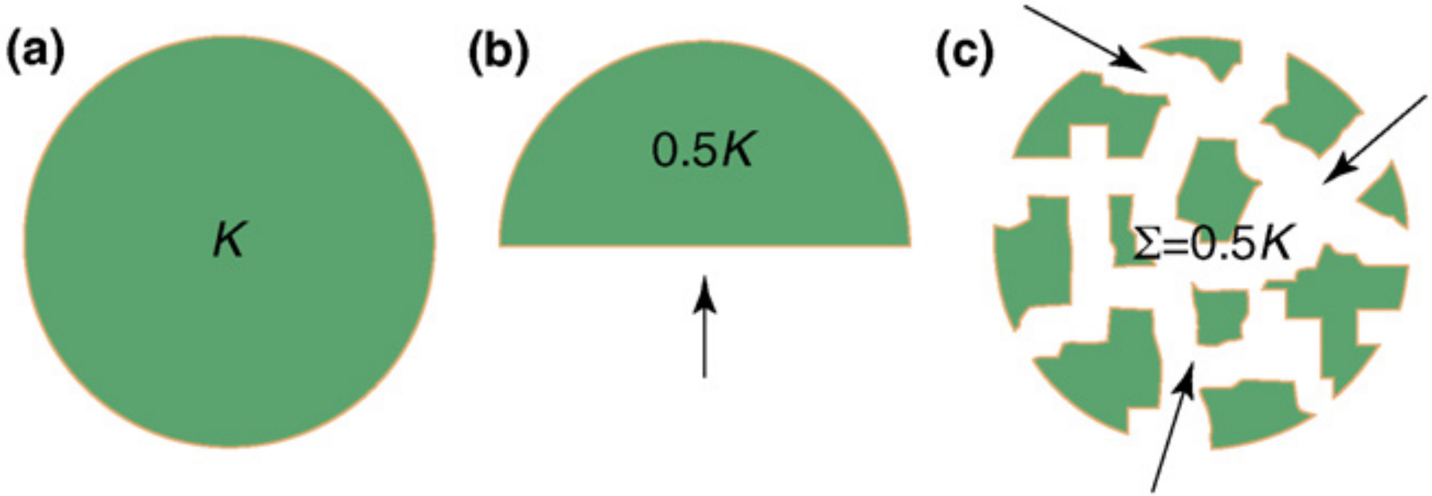
Duration as a predictor of risk

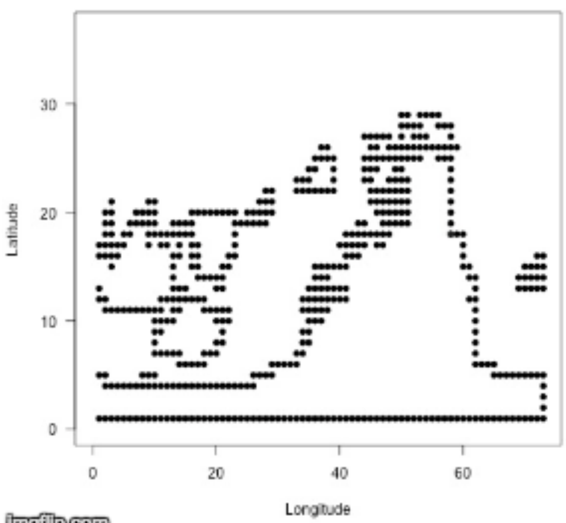
- Older species tend to be more resistant to extinction.
- A few different hypotheses are commonly floated about this.
  - You are old because you have some other extinction-resistant trait that let you be old.
  - Older species become more adapted over time.
  - Older species are not really old.

Habitat fragmentation

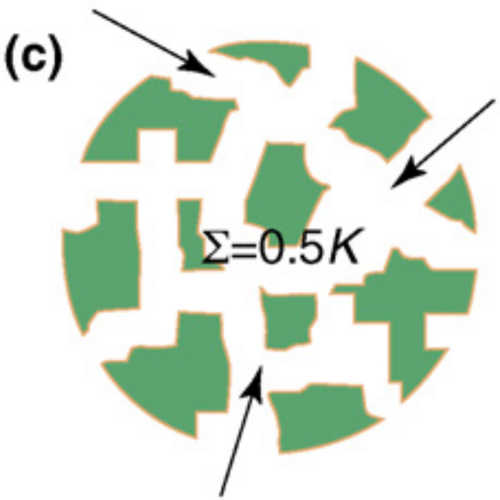


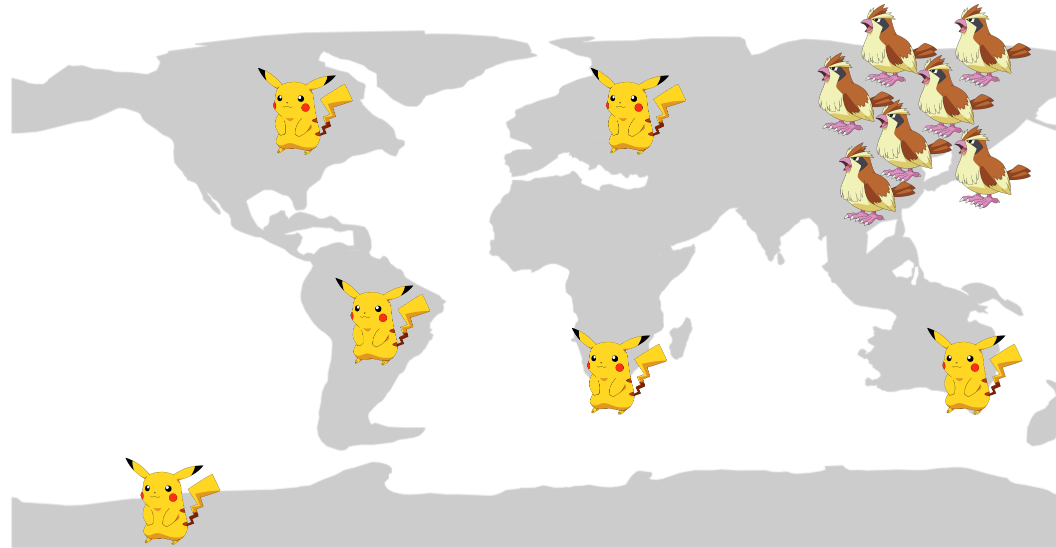
Habitat fragmentation

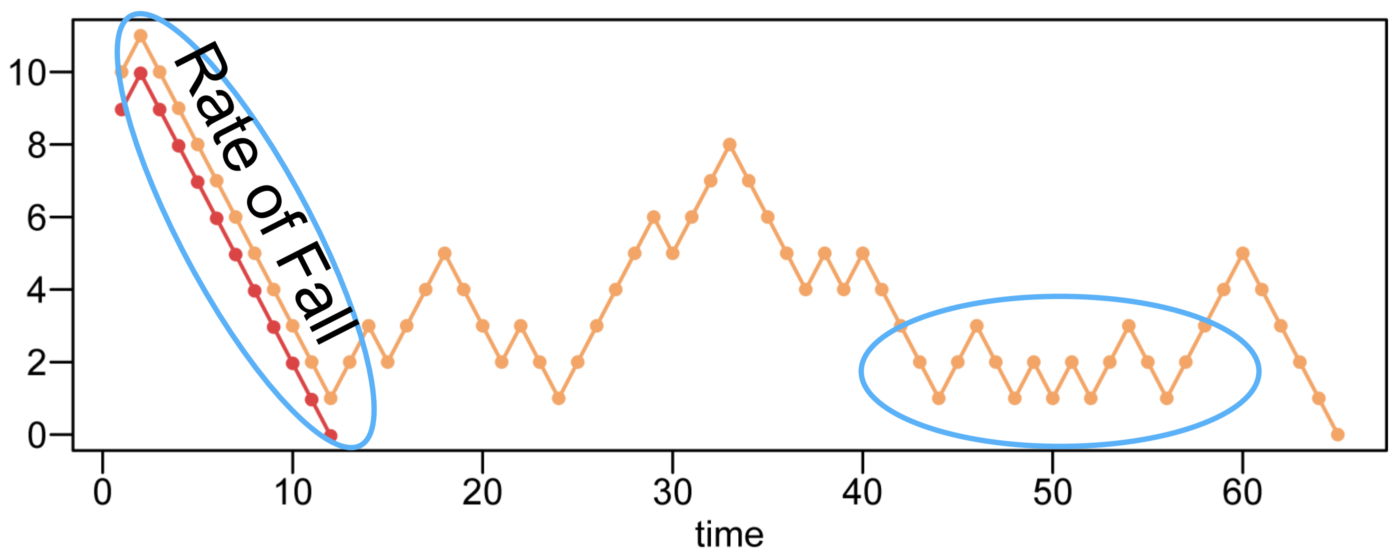




Modern conservation biology







IUCN RED LIST

What is a determinant?

- Heavily hunted in the mid-1800s, eventually there were no heath hens on the mainland, and only a small population survived on Martha’s Vineyard
- A large fire destroyed much of their breeding area on the island.
- An unusual influx of predatory goshawks the following year.
- The introduction of a poultry disease from domesticated turkeys.
- Heath Hens were extinct by around 1932