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1 PATHS TO STATISTICAL FLUENCY FOR ECOLOGISTS

2
3 Aaron M. Ellison^{1,3} & Brian Dennis²

4
5 ¹Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366

6 ²Department of Fish & Wildlife Resources, and Department of Statistics, University of Idaho,

7 Moscow, ID 83844

8 ³For all correspondence: aellison@fas.harvard.edu

9
10 ABSTRACT

11 Twenty-first century ecology requires statistical fluency. Observational and experimental
12 studies routinely gather non-Normal, multivariate data at many spatiotemporal scales.
13 Experimental studies routinely include multiple blocked and nested factors. Ecological theories
14 routinely incorporate both deterministic and stochastic processes. Ecological debates frequently
15 revolve around choices of statistical analyses. Our journals are replete with likelihood and state-
16 space models, Bayesian and frequentist inference, complex multivariate analyses, and papers on
17 statistical theory and methods. We test hypotheses, model data, and forecast future environmental
18 conditions. And many *appropriate* statistical methods are not automated in software packages. It
19 is time for ecologists to understand statistical modeling well enough to construct nonstandard
20 statistical models and apply various types of inference – estimation, hypothesis testing, model
21 selection, and prediction – to our models and scientific questions. In short, ecologists need to
22 move beyond basic statistical literacy and attain statistical fluency.

23 ***In a nutshell:***

- 24 • Ecologists need to use nonstandard statistical models and methods of statistical inference to
25 test models of ecological processes and to address pressing environmental problems.
- 26 • Such statistical models of ecological processes include both deterministic and stochastic
27 parts, and statistically-fluent ecologists will need to use probability theory and calculus to fit
28 these models to available data.
- 29 • Many ecologists lack appropriate background in probability theory and calculus because
30 there are serious disconnections between the quantitative nature of ecology, the quantitative
31 skills we expect of ourselves and our students, and how we teach and learn quantitative
32 methods.
- 33 • A prescription for attaining statistical fluency includes: two semesters of standard calculus; a
34 calculus-based introductory statistics course; a two-course sequence in probability and
35 mathematical statistics; and most importantly, a commitment to using calculus and post-
36 calculus statistics in courses in ecological and environmental-science curricula.

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38

INTRODUCTION

39 For the better part of a century, ecology has used statistical methods developed mainly for
40 agricultural field trials by statistics luminaries such as Gossett, Fisher, Neyman, Cochran, and
41 Cox (Gotelli and Ellison 2004). Calculation of sums of squares was just within the reach of
42 mechanical (or human) calculators (Fig. 1), and generations of ecologists have spent many hours
43 in their labor of love: caring and curating the results of analysis of variance (ANOVA) models.
44 Basic linear models (ANOVA and regression) continue to be the dominant mode of ecological
45 data analysis; they were used in 75% of all papers published in *Ecology* in 2008 ($N = 344$; 24

46 papers were excluded from the analysis because they were conceptual overviews, notes, or
47 commentaries that reported no statistics at all). These methods are employed most appropriately
48 to analyze relatively straightforward experiments aimed at estimating the magnitudes of a small
49 number of additive fixed effects or testing simple statistical hypotheses. Although the vast
50 majority of papers published in *Ecology* test statistical hypotheses (75% reported at least one *P*-
51 value) and estimate effect sizes (69%), only 32% provided assessments of uncertainty (*e.g.*,
52 standard errors, confidence intervals, probability distributions) on the estimates of the effect sizes
53 themselves (as distinguished from the common practice of reporting standard errors of observed
54 means).

55 But these methods do not reflect ecologists' collective statistical needs for the 21st
56 century. How can we use ANOVA and simple linear regression to forecast ecological processes
57 in a rapidly changing world (Clark *et al.* 2001)? Familiar examples or ecological problems that
58 would benefit from sophisticated modeling approaches include: forecasts of crop production;
59 population viability analyses; prediction of the spread of epidemics or invasive species; and
60 predictions of fractionation of isotopes through food webs and ecosystems. Such forecasts, and
61 many others like them, are integral to policy instruments such as the Millennium Ecosystem
62 Assessment (2005) or the IPCC reports (IPCC 2007). Yet such forecasts and similar types of
63 studies are uncommon in top-tier ecological journals. Why? Do ecologists limit their study
64 designs so as to produce data that will fit into classical methods of analysis? Are nonstandard
65 ecological data sometimes mis-analyzed with off-the-shelf statistical techniques (Bolker *et al.*
66 2009)? In the statistical shoe store, do ecologists sometimes cut the foot to fit the shoe? How do
67 we learn to do more than determine *P*-values associated with mean squared error terms in
68 analysis of variance (Butcher *et al.* 2007)?

69 The short answer is by studying and using “models”. Statistical analysis is fundamentally
70 a process of building and evaluating stochastic models, but such models were hidden or even
71 forbidden in the agricultural statistics-education tradition that emphasized practical training and
72 de-emphasized calculus. Yet, any ecological process producing variable data can (and should) be
73 described using a stochastic, statistical model (Bolker 2008). Such models may start as a
74 conceptual or “box-and-arrow” diagram, but these should then be turned into more quantitative
75 descriptions of the processes of interest. The building blocks of such quantitative descriptions are
76 deterministic formulations of the hypothesized effects of environmental variables, time, and
77 space, coupled with discrete and continuous probability distributions. These distributions, rarely
78 Normal, are chosen by the investigator to describe how the departures of data from the
79 deterministic sub-model are hypothesized to occur. The Sums of Squares – a surrogate for
80 likelihood in Normal distribution models – is no longer the only statistical currency; likelihood
81 and other such statistical objective functions are the more widely useful coins of the realm.

82 Alternatives to parametric model-based methods include non-parametric statistics and
83 machine-learning. Classical non-parametric statistics (Conover 1998) have been supplanted by
84 computer simulation and randomization tests (Manly 2006) but the statistical or causal models
85 that they test are rarely apparent to data analysts and users of packaged (especially compiled)
86 software products. Similarly, model-free machine-learning and data-mining methods (Breiman
87 2001) seek large-scale correlative patterns in data by letting the data “speak for themselves”.
88 Although the adherents of these methods promise that machine-learning and data-mining will
89 make the “standard” approach to scientific understanding – hypothesis → model → test –
90 obsolete (Anderson 2008), the ability of these essentially correlative methods to advance
91 scientific understanding and provide reliable forecasts of future events has yet to be

92 demonstrated. Thus we focus here on the complexities inherent in fitting stochastic statistical
93 models, estimating their parameters, and carrying out statistical inference on the results.

94 Our students and colleagues create or work far less frequently with stochastic statistical
95 models than they use routine ANOVA and its relatives; in 2008, only 23% of papers published in
96 *Ecology* used stochastic models or applied competing statistical models on their data (and about
97 half of these used automated software such as stepwise regression or MARK [White and
98 Burnham 1999] that take much of the testing out of the hands of the user to contrast among
99 models constructed from many possible combinations of parameters). Why? It may be that we
100 (or at least those of us who publish in our leading journals) primarily conduct well designed
101 experiments that test one or two factors at a time and have sufficient sample sizes and balance
102 among treatments to satisfy all the requirements of ANOVA and yield high statistical power. If
103 this is true, the complexity of stochastic models is simply unnecessary. But our data rarely are so
104 forgiving; more frequently our sample sizes are too small, our data are not Normally distributed
105 (or even continuous), our experimental and observational designs include mixtures of fixed and
106 random effects, and we know that process affect our study systems hierarchically. And finally,
107 we want to do more with our data than simply tell a good story. We want to generalize, predict,
108 and forecast. In short, we really *do* need to model our data.

109 We suggest that there are profound disconnections between the quantitative nature of
110 ecology, the quantitative (mathematical and statistical) skills we expect of ourselves and of our
111 students, and how we teach and learn quantitative methods. We illustrate these disconnections
112 with two motivating examples and suggest a new standard – *statistical fluency* – for quantitative
113 skills that are learned and taught by ecologists. We close by providing a prescription for better
114 connecting (or reconnecting) our teaching with the quantitative expectations we have for our

115 students so that ecological science can progress more rapidly and with more relevance to society
116 at large.

117

118 TWO MOTIVATING EXAMPLES

119 *The first law of population dynamics*

120 Under optimal conditions, populations grow exponentially:

$$121 \quad N_t = N_0 e^{rt} \quad (\text{Eqn. 1})$$

122 In this equation, N_0 is the initial population size, N_t is the population size at time t , r is the
123 instantaneous rate of population growth (units of individuals per infinitesimally small units of
124 time t), and e is the base of the natural logarithm. This simple equation is often referred to as the
125 first law of population dynamics (Turchin 2001) and it is universally presented in undergraduate
126 ecology textbooks. Yet we all know all too well that students in our introductory ecology classes
127 view exponential growth mainly through glazed eyes. Why? Equation 1 is replete with complex
128 mathematical concepts normally encountered in the first semester of calculus: the concept of a
129 function, raising a real number to a real power, and Euler's number e . But the majority of
130 undergraduate ecology courses *do not require* calculus as a prerequisite, thereby insuring that
131 understanding fundamental concepts such as exponential growth is not an expected course
132 outcome. The current financial meltdown associated with the foreclosure of exponentially
133 ballooning sub-prime mortgages illustrates writ large Albert Bartlett's assertion that "the greatest
134 shortcoming of the human race is our inability to understand the exponential function". Surely
135 ecologists can do better.

136 Instructors of undergraduate ecology courses that do require calculus as a prerequisite
137 often find themselves apologizing to their students that ecology is a quantitative science and go

138 on to provide conceptual or qualitative workarounds that keep course enrollments high and deans
139 happy. Students in the resource management fields – forestry, fisheries, wildlife, *etc.* – suffer
140 even more, as quantitative skills are further de-emphasized in these fields. Yet resource managers
141 need a deeper understanding of exponential growth (and other quantitative concepts) than do
142 academic ecologists; for example, the relationship of exponential growth to economics or its role
143 in the concept of the present value of future revenue. The result in all these cases is the
144 perpetuation of a *culture of quantitative insecurity* among many students.

145 The actual educational situation with our example of population growth models in
146 ecology is much worse. The exponential growth expression as understood in mathematics is the
147 solution to a differential equation. Differential equations, of course, are a core topic of calculus.
148 Indeed, because so many dynamic phenomena in all scientific disciplines are naturally modeled
149 in terms of instantaneous forces (rates), the topic of differential equations is one of the main
150 reasons for studying calculus in the first place! To avoid introducing differential equations to
151 introductory ecology classes, most ecology textbooks present exponential growth in a discrete-
152 time form: $N_{t+1} = (1 + \text{births} - \text{deaths}) N_t$ and then miraculously transmogrify this (with little or
153 no explanation) into the continuous time model given by $dN/dt = rN$. The attempts at intuition
154 obscure, for instance, the exact nature of the quantities “births” and “deaths” and how they
155 would be measured, not to mention the assumptions involved in discrete time versus continuous
156 time formulations.

157 Furthermore, Eqn. 1 provides no insights into how the unknown parameters (r and even
158 N_0 when population size is not known without error) ought to be estimated from ecological data.
159 To convince yourself that it is indeed difficult to estimate unknown parameters from ecological
160 data, consider the following as a first exercise for an undergraduate ecology laboratory: for a

161 given set of demographic data (perhaps collected from headstones in a nearby cemetery),
162 estimate r and N_0 in Eqn. 1 and provide a measure of confidence in the estimates.

163 Finally, to actually use Eqn. 1 to describe the exponential growth of a real population, one
164 must add stochasticity by modeling departures of observed data from the model itself. There are
165 many different ways of modeling such variability that depend on the specific stochastic forces
166 acting on the observations; each model gives a different likelihood function for the data and
167 thereby prescribes a different way for estimating the growth parameter. In addition, the choices
168 of models for the stochastic components, such as demographic variability, environmental
169 variability, and sampling variability, must be added to (and evaluated along with) the suite of
170 modeling decisions concerning the deterministic core, such as changing exponential growth to
171 some density dependent form or adding a predator. Next, extend these concepts and methods to
172 “simple” Lotka-Volterra models of competition and predation...

173

174 *The Cumulative Distribution Function for a Normal curve*

175 Our second motivating example deals with a core concept of statistics:

176
$$\int_a^b (\sigma^2 2\pi)^{-1/2} \exp\left[-\frac{(y-\mu)^2}{2\sigma^2}\right] dy = \Phi(b) - \Phi(a) \quad (\text{Eqn. 2})$$

177 The function $\Phi(y)$ is the cumulative distribution function for the Normal distribution and Eqn. 2
178 describes the area under a Normal curve (with two parameters: mean = μ and variance = σ^2)
179 between a and b . This quantity is important because the Normal distribution is used as a model
180 assumption for many statistical methods (e.g., linear models, probit analysis), and Normal
181 probabilities can express predicted frequencies of occurrence of observed events (data). Also,
182 many test statistics also have sampling distributions that are approximately Normal. Rejection

183 regions, P -values, and confidence intervals all are defined in terms of areas under a Normal
184 curve.

185 The meaning, measurement, and teaching of P -values continues to bedevil statisticians
186 (e.g., Berger 2003, Hubbard and Byarri 2003, Murdoch *et al.*, 2008), yet ecologists often use and
187 interpret probability and P -values uncritically, and few ecologists can clearly describe a
188 confidence interval with any degree of... uh, confidence. To convince yourself that this is a real
189 problem, consider asking any graduate student in ecology (perhaps during their oral
190 comprehensive examination) to explain why $P(10.2 < \mu < 29.8) = 0.95$ is not the correct
191 interpretation of a confidence interval on the parameter μ (original equation from Poole 1974);
192 odds are you will get an impression of someone who is not secure in their statistical
193 understanding. Bayesians should refrain for chortling about the transparency of credible sets.
194 Interpreting Bayesian credible intervals makes equally large conceptual demands (Hill 1968,
195 Lele and Dennis 2009). When pushed, students can *calculate* a confidence interval by hand or
196 with computer software. But interpreting it (Box 1) and generalizing its results is where the
197 difficulty lies.

198 Three centuries of study of Eqn. 2 by mathematicians and statisticians have not reduced it
199 to any simpler form, and evaluating it for any two real numbers a and b must be done
200 numerically. Alternatively, one can proceed through the mysterious, multi-step table-look-up
201 process, involving the Z -tables provided in the back of every basic statistics text. Look-up tables
202 or built-in functions in statistical software may work fine for standard probability distributions
203 such as the Normal or F distribution, but what about non-standard distributions or mixtures of
204 distributions used in many hierarchical models? Numerical integration is a standard topic in
205 calculus classes, and it can be applied to *any* distribution of interest, not just the area under a

206 Normal curve. Consider the power of understanding: how areas under curves can be calculated
207 for other continuous models besides the Normal distribution; how the probabilities for other
208 distributions sometimes converge to the above form based on the Normal; and how Normal-
209 based probabilities can serve as building blocks for hierarchical models of more complex data
210 (Clark 2007). Such interpretation and generalization is at the heart of statistical fluency.

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212

DEVELOPING STATISTICAL FLUENCY AMONG ECOLOGISTS

213

Fluency defined

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We use the term “fluency” to emphasize that a deep understanding of statistics and statistical concepts differs from “literacy” (Table 1). Statistical literacy is a common goal of introductory statistics courses that presuppose little or no familiarity with basic mathematical concepts introduced in calculus, but it is insufficient for 21st century ecologists. Like fluency in a foreign language, statistical fluency means not only a sufficient understanding of core theoretical concepts (grammar in languages, mathematical underpinnings in statistics) but also the ability to apply statistical principles and adapt statistical analyses for nonstandard problems (Table 1).

We must recognize that calculus is the language of the general principles that underlie probability and statistics. We emphasize that statistics is *not* mathematics; rather, like physics, statistics uses a lot of mathematics (De Veaux and Velleman 2008). And ecology uses a lot of statistics. But the conceptual ideas of statistics are *really hard*. Basic statistics contains abstract notions derived from those in basic calculus, and students who take calculus courses *and use* calculus in their statistics courses have a deeper understanding of statistical concepts and the confidence to apply them in novel situations. In contrast, students who take only calculus-free,

228 cookbook-style statistical methods courses often have a great deal of difficulty adapting the
229 statistics that they know to ecological problems for which those statistics are inappropriate.

230 For ecologists, the challenge of developing statistical fluency has moved well beyond the
231 relatively simple task of learning and understanding fundamental aspects of contemporary data
232 analysis. The very theories themselves in ecology include stochastic content that can only be
233 interpreted probabilistically and include parameters that can only be estimated using complex
234 statistics. For example, conservation biologists struggle with (and frequently mis-express) the
235 distinctions between demographic and environmental variability in population viability models
236 and must master the intricacies of first passage properties of stochastic growth models.
237 Community ecologists struggle to understand (and figure out how to test) the “neutral” model of
238 community structure (Hubbell 2001), itself related to neutral models in genetics (see Leigh 2007)
239 with which ecological geneticists must struggle. Landscape ecologists must struggle with
240 stochastic dispersal models and spatial processes. Behavioral ecologists must struggle with
241 Markov chain models of behavioral states. All must struggle with huge individual-based
242 simulations and hierarchical (random or latent effects) models. No subfield of ecology, no matter
243 how empirical the tradition, is safe from encroaching stochasticity and the attendant need for the
244 mathematics and statistics to deal with it.

245

246 *Statistics is a post-calculus subject*

247 What mathematics do we need – to create, parameterize, and use stochastic statistical
248 models of ecological processes? At a minimum, we need calculus. We must recognize that
249 statistics is a post-calculus subject and that calculus is a prerequisite for development of
250 statistical fluency. Expectation, conditional expectation, marginal and joint distributions,

251 independence, likelihood, convergence, bias, consistency, distribution models of counts based on
252 infinite series... are key concepts of statistical modeling that must be understood by practicing
253 ecologist, and these are straightforward calculus concepts. No amount of pre-calculus statistical
254 “methods” courses can make up for this fact. Calculus-free statistical methods courses doom
255 ecologists to a lifetime of insecurity with regard to the ideas of statistics. Such courses are like
256 potato chips: virtually no nutritional value, no matter how many are consumed. Pre-calculus
257 statistics courses are similar to pre-calculus physics courses in that regard; both have reputations
258 for being notorious, unsatisfying parades of mysterious plug-in formulas. Ecologists who have
259 taken and internalized post-calculus statistics courses are ready to grapple with the increasingly
260 stochastic theories at the frontiers of ecology and will be able to rapidly incorporate future
261 statistical advances in their kit of data analysis tools. How do our students achieve statistical
262 fluency?

263

264 *The prescription*

265 Basic calculus, including an introduction to differential equations, seems to us to be a
266 minimum requirement. Our course prescription includes (1) two semesters of standard calculus
267 and an introductory, calculus-requiring introductory statistics course in college; and (2) a two-
268 semester post-calculus sequence in probability and mathematical statistics in the first or second
269 year of graduate school (Box 2). But it is not enough to simply *take* calculus courses, as calculus
270 already is clearly required (or at least recommended) by virtually all undergraduate science
271 degree programs (Fig. 2). Rather, calculus must be *used*; not only in statistics courses taken by
272 graduate students in ecology but most importantly in undergraduate and graduate courses in
273 ecology (including courses in resource management and environmental science)! If this seems

274 overly daunting, consider that Hutchinson (1978) summarizes “the modicum of infinitesimal
275 calculus required for ecological principles” in three and a half pages. Contemporary texts (such
276 as Clark 2007 or Bolker 2008) in ecological statistical modeling use little more than single
277 variable calculus and basic matrix algebra. Like Hutchinson, Bolker (2008) covers the essential
278 calculus and matrix algebra in 4 pages, each half the size of Hutchinson’s! Clark’s (2007) 100-
279 page mathematical refresher is somewhat more expansive, but in all cases the authors illustrate
280 that knowledge of some calculus allows one to advance rapidly on the road to statistical fluency.

281 We emphasize that nascent ecologists need not take *more* courses to attain statistical
282 fluency; they just need to take courses that are *different* from standard “methods” classes.
283 Current graduate students may need to take refresher courses in calculus and mathematical
284 statistics, but we expect that our prescription (Box 2) will actually reduce the time that future
285 ecology students spend in mathematics and statistics classrooms. Most undergraduate life science
286 students already take calculus and introductory statistics (Fig. 2). The pre-calculus statistical
287 methods courses that are currently required can be swapped out in favor of two semesters of
288 post-calculus probability and statistics. Skills in particular statistical methods can be obtained
289 through self-study or through additional methods courses; a strong background in probability and
290 statistical theory makes self-study a realistic option for rapid learning for motivated students.

291

292 *Why not just collaborate with professional statisticians?*

293 In the course of speaking about statistics education to audiences of ecologists and natural
294 resource scientists, we often are asked questions such as: “I don’t have to be a mechanic to drive
295 a car, so why do I need to understand statistical theory to be an ecologist? (and why do I have to
296 know calculus to do statistics?)” Our answer, the point of this article, is that the analogy of

297 statistics as a tool or black box increasingly is failing the needs of ecology. Statistics is an
298 essential part of the thinking, the hypotheses, and the very theories of ecology. Ecologists of the
299 future should be prepared to confidently use statistics so that they can make substantial progress
300 at the frontiers of our science.

301 “But,” continues the questioner, “why can’t I just enlist the help of a statistician?”

302 Collaborations with statisticians can produce excellent results and should be encouraged
303 wherever and whenever possible, but ecologists will find that their conversations and interactions
304 with professional statisticians will be enhanced if ecologists have done substantial statistical
305 ground work before their conversation begins and if both ecologists and statisticians speak a
306 common language (mathematics!). Collaborations between ecologists and statisticians also can
307 be facilitated by building support for consulting statisticians into grant proposals; academic
308 statisticians rely on grant support as much as academic ecologists do. However, ecologists cannot
309 count on the availability of statistical help whenever it is needed. And, statistical help may be
310 unavailable at many universities. Thus, we believe that ecologists should be self-sufficient and
311 self-assured. We should master our own scientific theories and be able to discuss with confidence
312 how our conclusions are drawn from ecological data. We should be knowledgeable enough to
313 recognize what we do understand and what we do not, learn new methods ourselves, and seek
314 out experts who can help us increase our understanding.

315

316 CONCLUSION: MATHEMATICS AS THE LANGUAGE OF ECOLOGICAL NARRATIVES

317 It is increasingly appreciated that scientific concepts can be communicated to students of
318 all ages through stories and narratives (Fig. 3; see also Molles 2006). We do not disagree with the
319 importance of telling a good story and engaging our students with detailed narratives of how the

320 world works. Nor do we minimize the importance of doing “hands-on” ecology through inquiry-
321 based learning, which is both important and fun. Field trips, field work, and lab work are exciting
322 and entertaining, draw students into ecology, and dramatically enhance ecological literacy. For
323 individuals who pursue careers in fields outside of science, qualitative experiences and an
324 intuitive grasp of the story-line can be sufficient (Cope 2006). But for our students who want the
325 deepest appreciation and joy of how science works – understanding how we know what we know
326 – and for those of us who are in scientific careers and are educating the next generation of
327 scientists, we should use the richest possible language for our narratives of science. And that
328 language is mathematics.

329

330

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337

338

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406 marked animals. *Bird Study* **46 (Supp.)**: 120-138.

407 **Table 1.** The different components and stages of statistical literacy.* “Process” refers to a
 408 statistical concept (such as a *P*-value or confidence interval) or method.

Basic literacy	Ability to reason statistically	Fluency in statistical thinking
Identify the process		Apply the process to new situations
Describe it	Explain the process	Critique it
Rephrase it	Why does it work?	Evaluate it
Translate it	How does it work?	Generalize from it
Interpret it		

409 * modified from delMas 2002

410 Figure Legends

411 **Figure 1** – *Milestones in statistical computing. A. Women (ca. 1920) in the Computing Division*
412 *of the U.S. Department of the Treasury (or the Veterans' Bureau) determining the bonuses to be*
413 *distributed to veterans of World War I. Photograph from the Library of Congress Lot 12356-2,*
414 *negative LC-USZ62-101229. B. Professor (and Commander) Howard Aiken, Lieutenant (and*
415 *later Rear Admiral) Grace Hopper, and Ensign Campbell in front of a portion of the Mark I*
416 *Computer. The Mark I was designed by Aiken, built by IBM, fit in a steel frame 16 m long × 2.5*
417 *m high, weighed approximately 4,500 kg, and included 800 km of wire, It was used to solve*
418 *integrals required by the U.S. Navy Bureau of Ships during World War II, and physics problems*
419 *associated with magnetic fields, radar, and the implosion of early atomic weapons. Grace*
420 *Hopper was the lead programmer of the Mark I. Her experience developing its programs led her*
421 *to develop the first compiler for a computer programming language (which subsequently evolved*
422 *into COBOL), and she developed early standards for both the FORTRAN and COBOL*
423 *programming languages. The Mark I was programmed using punched paper tape and was the*
424 *first automatic digital computer in the U.S. Its calculating units were mechanically synchronized*
425 *by an ~ 15-m long drive shaft connected to a 4 kW (5 horsepower) electric motor. The Mark I is*
426 *considered to be the first universal calculator (Stoll 1983). Photograph from the Harvard*
427 *University Office of News and Public Affairs, Harvard University Archives call number HUPSF*
428 *Computers (2), and reproduced with permission of the Harvard University Archives. C. A ca.*
429 *2007 screen-shot of the open-source R statistical package running on a personal computer. The*
430 *small, notebook computers that on which we run R and other statistical software every day have*
431 *central processors that execute 10,000 – 100,000 MIPS (million instructions per second). In*
432 *contrast, the earliest commercial computers executed 0.06-1.0 KIPS (thousand instructions per*

433 *second), and Harvard's Mark I computer took approximately 6 seconds to simply multiply two*
434 *numbers together; computing a single logarithm took more than a minute. (Image from*
435 *<http://www.r-project.org>, copyright the R Foundation, and used with permission).*

436

437 **Figure 2** - *Total number of quantitative courses, calculus courses, and statistics courses required*
438 *at the 25 liberal-arts colleges and universities that produce the majority of students who go on to*
439 *receive Ph.D.s in the life sciences. Institutions surveyed are based on data from the National*
440 *Science Foundation (1996). Data collected from department web sites and college or university*
441 *course catalogs, July 2008.*

442

443 **Figure 3** – *Telling a compelling ecological story requires quantitative data. Here, Harvard*
444 *Forest researcher Julian Hadley describes monthly cycles of carbon storage in hemlock and*
445 *hardwood stands. The data are collected at 10-20 Hz from three eddy-covariance towers,*
446 *analyzed and summarized with time-series modeling, and incorporated into regional estimates*
447 *(e.g., Matross et al. 2006) and forecasts (e.g., Desai et al. 2007), and used to determine regional*
448 *and national carbon emissions targets and policies. Photograph by David Foster, and used with*
449 *permission of the Harvard Forest Archives.*



450

451 Figure 1A

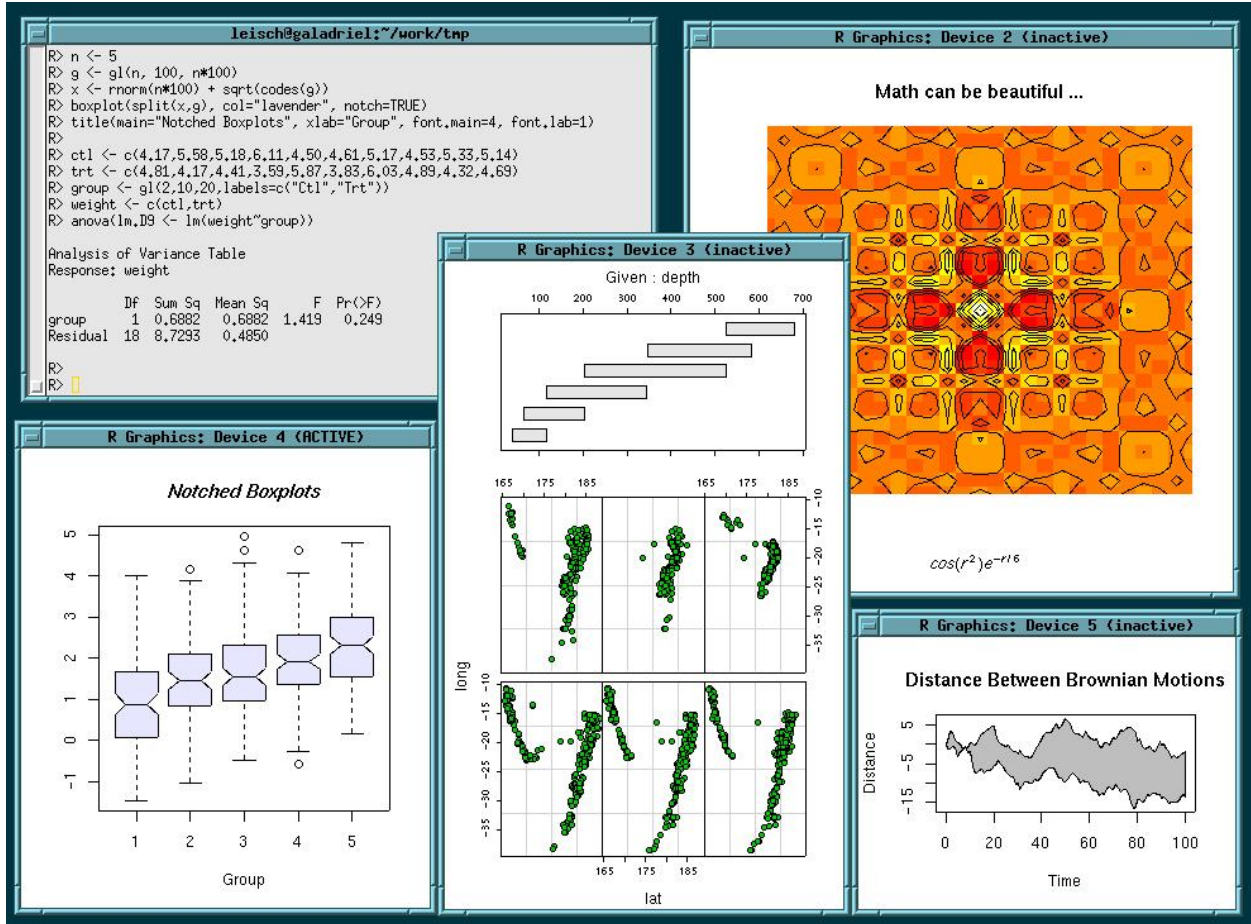
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454 Figure 1B

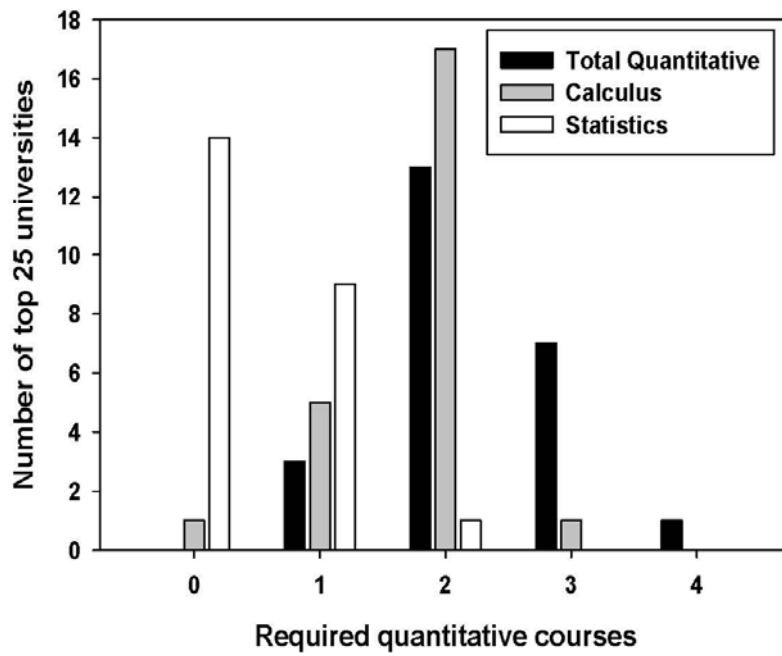
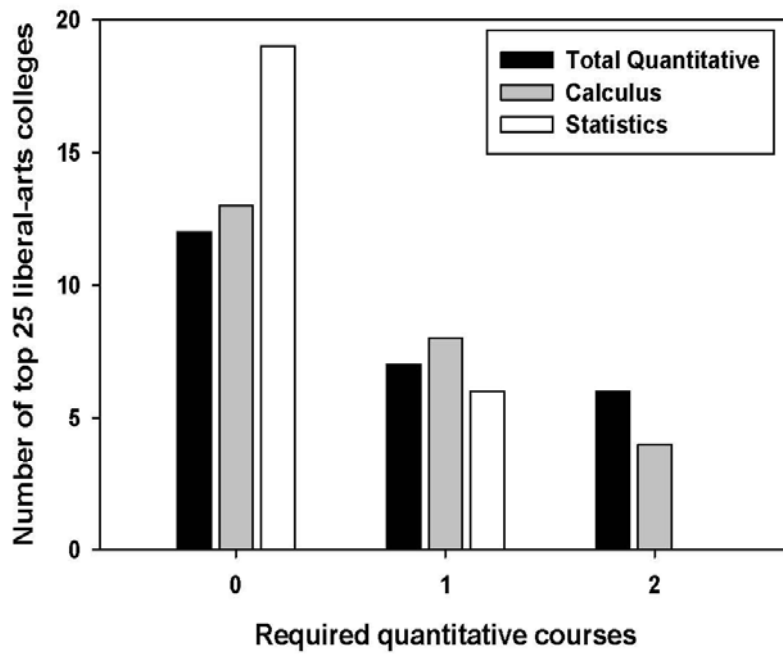
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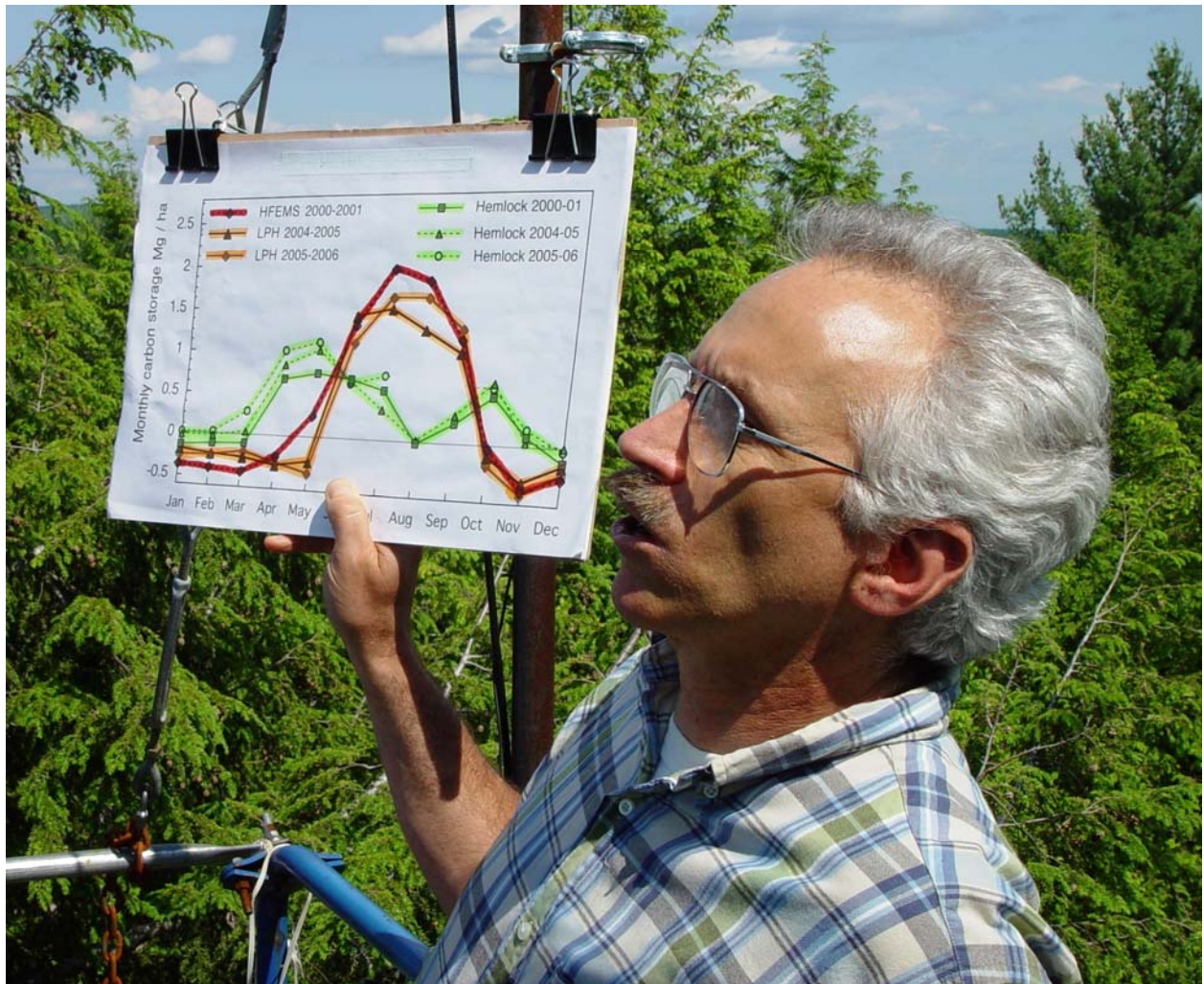
Figure 1C



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Fig. 2



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Figure 3.

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451 **Box 1. Why “ $P(10.2 < \mu < 29.8) = 0.95$ ” is not a correct interpretation of confidence**
452 **interval, and what are confidence intervals, anyway?**

453 This statement says that the probability that the true population mean μ lies in the interval
454 (10.2, 29.8) equals 0.95. But μ is a fixed (but unknown) constant: it is either in the interval (10.2,
455 29.8) or it is not. The probability that μ is in the interval is zero or one; we just do not know
456 which. A confidence interval actually asserts that 95% of the confidence intervals resulting from
457 hypothetical repeated samples (taken under the same random sampling protocol used for the
458 single sample) will contain μ in the long run. Think of a game of horseshoes in which you have
459 to throw the horseshoe over a curtain positioned so that you cannot see the stake. You throw a
460 horseshoe and it lands (thud!); the probability is zero or one that it is a ringer, but you do not
461 know which. The confidence interval arising from a single sample is the horseshoe on the
462 ground, and μ is the stake. If you had the throwing motion practiced so that the long run
463 proportion of successful ringers was 0.95, then your horseshoe game process would have the
464 probabilistic properties claimed by 95% confidence intervals. You do not know the outcome
465 (whether or not μ is in the interval) on any given sample, but you have constructed the sampling
466 process so as to be assured that 95% of such samples in the long run would produce confidence
467 intervals that are ringers. The distinction is clearer when we write the probabilistic expression for
468 a 95% confidence interval:

469
$$P(L \leq \mu \leq U) = 0.95$$

470 What this equation is telling us is that the true (but unknown) population mean μ will be found
471 95% of the time in an interval bracketed by L at the lower end and U at the upper end, *where* L

472 *and U vary randomly from sample to sample.* Once the sample is drawn, the lower and upper
473 bounds of the interval are fixed (the horseshoe has landed), and μ (the stake) is either contained
474 in the interval or it is not.

475 Many standard statistical methods construct confidence intervals symmetrically in the
476 form of a “point estimate” plus or minus a “margin of error”. For instance, a $100(1 - \alpha)\%$
477 confidence interval for μ when sampling from a Normal distribution is constructed based on the
478 following probabilistic property:

$$479 \quad P(\bar{Y} - t_{\alpha/2} \sqrt{S^2/n} \leq \mu \leq \bar{Y} + t_{\alpha/2} \sqrt{S^2/n}) = (1 - \alpha) .$$

480 Here $t_{\alpha/2}$ is the percentile of a t-distribution with $n - 1$ degrees of freedom such that there is an
481 area of $\alpha/2$ under the t-distribution to the right of $t_{\alpha/2}$, and \bar{Y} and S^2 are respectively the
482 sample mean and sample variance of the observations. The quantities \bar{Y} and S^2 vary randomly
483 from sample to sample, making the lower and upper bounds of the interval vary as well. The
484 confidence interval itself becomes $\bar{y} \pm t_{\alpha/2} \sqrt{s^2/n}$, in which the lowercase \bar{y} and s^2 are the
485 actual numerical values of sample mean and variance resulting from a single sample. In general,
486 modern-day confidence intervals for parameters in non-Normal models arising from
487 computationally intensive methods such as bootstrapping and profile likelihood are not
488 necessarily symmetric around the point estimates of those parameters.

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Box 2. A prescription for statistical fluency.

The problem of how to use calculus in the context of developing statistical fluency can be solved *easily* and *well* by rearranging courses and substituting different statistics courses (those hitherto rarely taken by ecologists) for many of the statistical methods courses now taken in college and graduate school. The suggested courses are standard ones, with standard textbooks, and already exist at most universities. Our prescription is as follows.

For *undergraduate majors* in the ecological sciences (including “integrative biology”, ecology, evolutionary biology), along with students bound for scientific careers in resource management fields such as wildlife, fisheries, and forestry:

1. **At least two semesters of standard calculus.** “Standard” means real calculus, the courses taken by students in physical sciences and engineering. Those physics and engineering students go on to take a third (multivariable calculus) and a fourth semester (differential equations) of calculus, but these latter courses are not absolutely necessary for ecologists. Only a small amount of the material in those additional courses is used in subsequent statistics or ecology courses and can be introduced in those courses or acquired through self-study. Most population models must be solved numerically, methods for which can be covered in the population ecology courses themselves. (Please note we do not wish to discourage additional calculus for those students interested in excelling in ecological theory; our prescription, rather, should be regarded as minimum core for those who will ultimately have Ph.Ds in the ecological sciences, broadly defined.)

512 2. **An introductory statistics course which lists calculus as a prerequisite.** This course is
513 standard everywhere; it is the course that engineering and physical science students take,
514 usually as juniors. A typical textbook is Devore (2007).

515 3. **A commitment to using calculus and post-calculus statistics in courses in life-science**
516 **curricula** must go hand-in-hand with course requirements in calculus and post-calculus
517 statistics. Courses in the physical sciences for physical science majors use the language of
518 science – mathematics – and its derived tool – statistics – unapologetically, starting in
519 beginning courses. Why don't ecologists or other life scientists do the same? The basic
520 ecology course for majors should include calculus as a prerequisite and must use calculus
521 so that students see its relevance.

522

523 For *graduate students* in ecology (*sensu lato*):

524 1. **A standard two-course sequence in probability and mathematical statistics.** This sequence
525 is usually offered for undergraduate seniors and can be taken for graduate credit. Typical
526 textbooks are Rice (2006), Larson and Marx (2005), or Wackerly *et al.* (2007). The
527 courses usually require two semesters of calculus as prerequisites.

528 2. **Any additional graduate-level course(s) in statistical methods**, according to interests and
529 research needs. After a two-semester post-calculus probability and statistics sequence, the
530 material covered in many statistical methods courses also is amenable to self-study.

531 3. **Most ecologists will want to acquire some linear algebra** somewhere along the line, because
532 matrix formulations are used heavily in ecological and statistical theory alike. Linear
533 algebra could be taken either in college or graduate school. Linear algebra is often
534 reviewed extensively in courses such as multivariate statistical methods and population

535 ecology, and necessary additional material can be acquired through self-study. Those
536 ecologists whose research is centered on quantitative topics should consider formal
537 coursework in linear algebra.

538

539 The benefit of following this prescription is a rapid attainment of statistical fluency.
540 Whether students in ecology are focused more on theoretical ecology or on field methods,
541 conservation biology, or the interface between ecology and the social sciences, a firm grounding
542 in quantitative skills will make for better teachers, better researchers, and better interdisciplinary
543 communicators (for good examples see Armsworth *et al.* 2009 and other papers in the associated
544 special feature on “Integrating ecology and the social sciences” in the April 2009 issue of the
545 *Journal of Applied Ecology*). Since our prescription replaces courses rather than adds new ones,
546 the primary cost to swallowing this pill is either to recall and use calculus taken long ago or to
547 take a calculus refresher course.