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## Paths to Statistical Fluency for Ecologists

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1 PATHS TO STATISTICAL FLUENCY FOR ECOLOGISTS

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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 21<sup>st</sup>  
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 =  $\mu$  and variance =  $\sigma^2$ )  
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  $\mu$  (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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#### DEVELOPING STATISTICAL FLUENCY AMONG ECOLOGISTS

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##### *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 21<sup>st</sup> 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

#### REFERENCES

- 339 Anderson C. 2008. The Petabyte age: because more isn’t just more – more is different. *Wired*  
340 *Magazine* Issue **16.07** (July 2008):106-120.
- 341 Armsworth PR, Gaston KJ, Hanley ND, *et al.* 2009. Contrasting approaches to statistical  
342 regression in ecology and economics. *J Appl Ecol* **46**: 265-268.



343 Berger JO. 2003. Could Fisher, Jeffreys and Neyman have agreed on testing (with comments and  
344 rejoinder). *Stat Sci* **18**:1-32.

345 Bolker B. 2008. Ecological models and data in R. Princeton, NJ: Princeton University Press.

346 Bolker B, Brooks ME, Clark CJ, *et al.* 2009. Generalized linear mixed models: a practical guide  
347 for ecology and evolution. *Trends Ecol. Evol* **24**:127-135.

348 Breiman L. 2001. Statistical modeling: the two cultures (with discussion). *Stat. Sci* **16**:199-231.

349 Butcher JA, Groce JE, Lituma CM, *et al.* 2007. Persistent controversy in statistical approaches in  
350 wildlife sciences: a perspective of students. *J Wildlife Manage* **71**:2142-2144.

351 Clark JS. 2007. Models for ecological data: an introduction. Princeton, NJ: Princeton University  
352 Press.

353 Clark JS, Carpenter SR, Barber M, *et al.* 2001. Ecological forecasts: an emerging imperative.  
354 *Science* **293**:657-660.

355 Conover WJ. 1998. Practical nonparametric statistics, 3<sup>rd</sup> ed. New York: John Wiley and Sons.

356 Cope L. 2006. Understanding and using statistics. In: Blum D, Knudson M, and Henig RM  
357 (Eds). A field guide for science writers: the official guide of the National Association of  
358 Science Writers, 2<sup>nd</sup> ed. New York: Oxford University Press

359 delMas RC. 2002. Statistical literacy, reasoning, and learning: a commentary. *J Stat Ed* **10**.

360 De Veaux RD, and Velleman PF. 2008. Math is music; statistics is literature (or, why are there no  
361 six-year-old novelists?). *AmStat News* **September 2008**:54-58.

362 Desai A, Moorcroft PR, Bolstad PV and Davis KJ. 2007. Regional carbon fluxes from an  
363 observationally constrained dynamic ecosystem model: impacts of disturbance, CO<sub>2</sub>  
364 fertilization, and heterogeneous land cover. *J. Geophys Res* **112**: G01017

365 Devore JL. 2007. Probability and statistics for engineering and the sciences, 7<sup>th</sup> ed. Belmont, CA:  
366 Duxbury Press.

367 Gotelli NJ, and Ellison AM. 2004. A primer of ecological statistics. Sunderland, MA: Sinauer  
368 Associates.

369 Hill BM. 1968. Posterior distribution of percentiles: Bayes' theorem for sampling from a  
370 population. *J Am Stat Assoc* **63**:677-691.

371 Hubbard R, and Byarri MJ. 2003. Confusion over measures of evidence ( $p$ 's) versus errors ( $\alpha$ 's)  
372 in classical statistical testing (with discussion and rejoinder). *Am Stat* **57**:171-182.

373 Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. Princeton, NJ:  
374 University Press.

375 Hutchinson G.E. 1978. An introduction to population ecology. New Haven, CT: Yale University  
376 Press.

377 IPCC. 2007. Climate Change 2007: Synthesis report. Contribution of working groups I, II, and  
378 III to the fourth assessment report of the intergovernmental panel on climate change.  
379 Geneva: IPCC.

380 Larson RJ, and Marx ML. 2005. An introduction to mathematical statistics and its applications,  
381 4<sup>th</sup> ed. Upper Saddle River, NJ: Prentice-Hall.

382 Leigh, EG Jr. 2007. Neutral theory: a historical perspective. *J Evol Biol* **20**:2075-2091.

383 Lele SR, and Dennis B. 2009. Bayesian methods for hierarchical models: are ecologists making a  
384 Faustian bargain? *Ecol Appl* **19**:581-584.

385 Manly B.J.F. 2006. Randomization, bootstrap and Monte Carlo methods in biology, 3<sup>rd</sup> ed. Boca  
386 Raton, FL: CRC Press.

387 Matross DM *et al.* 2006. Estimating regional carbon exchange in New England and Quebec by  
388 combining atmospheric, ground-based and satellite data. *Tellus* **58B**: 344-358.

389 Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis.  
390 Washington, DC: Island Press.

391 Molles M. C. 2006. Ecology: concepts and applications, 4<sup>th</sup> edition. New York: McGraw-Hill.

392 Murdoch DJ., Tsai Y-L, and Adcock J. 2008. *p*-values are random variables. *Am Stat* **62**:242-  
393 245.

394 National Science Foundation. 1996. *Undergraduate origins of recent (1991-95) science and*  
395 *engineering doctorate recipients*, detailed statistical tables, NSF 96-334. Arlington,  
396 Virginia: National Science Foundation

397 Poole RW. 1974. An introduction to quantitative ecology. New York: McGraw-Hill.

398 Rice JA. 2006. Mathematical statistics and data analysis, 3<sup>rd</sup> edition. Belmont, CA: Duxbury  
399 Press.

400 Stoll EL. 1983. Mark I. In: Ralston A and Reilly ED (Eds.) Encyclopedia of computer science  
401 and engineering, 2<sup>nd</sup> ed. New York: Van Nostrand Reinhold.

402 Turchin P. 2001. Does population ecology have general laws? *Oikos* **94**:17-26.

403 Wackerly D, Mendenhall W, and Scheaffer RL. 2007. Mathematical statistics with applications,  
404 7<sup>th</sup> edition. Belmont, CA: Duxbury Press.

405 White GC and Burnham KP. 1999. Program MARK: Survival estimation from populations of  
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.

<b>Basic literacy</b>	<b>Ability to reason statistically</b>	<b>Fluency in statistical thinking</b>
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.*



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451 Figure 1A

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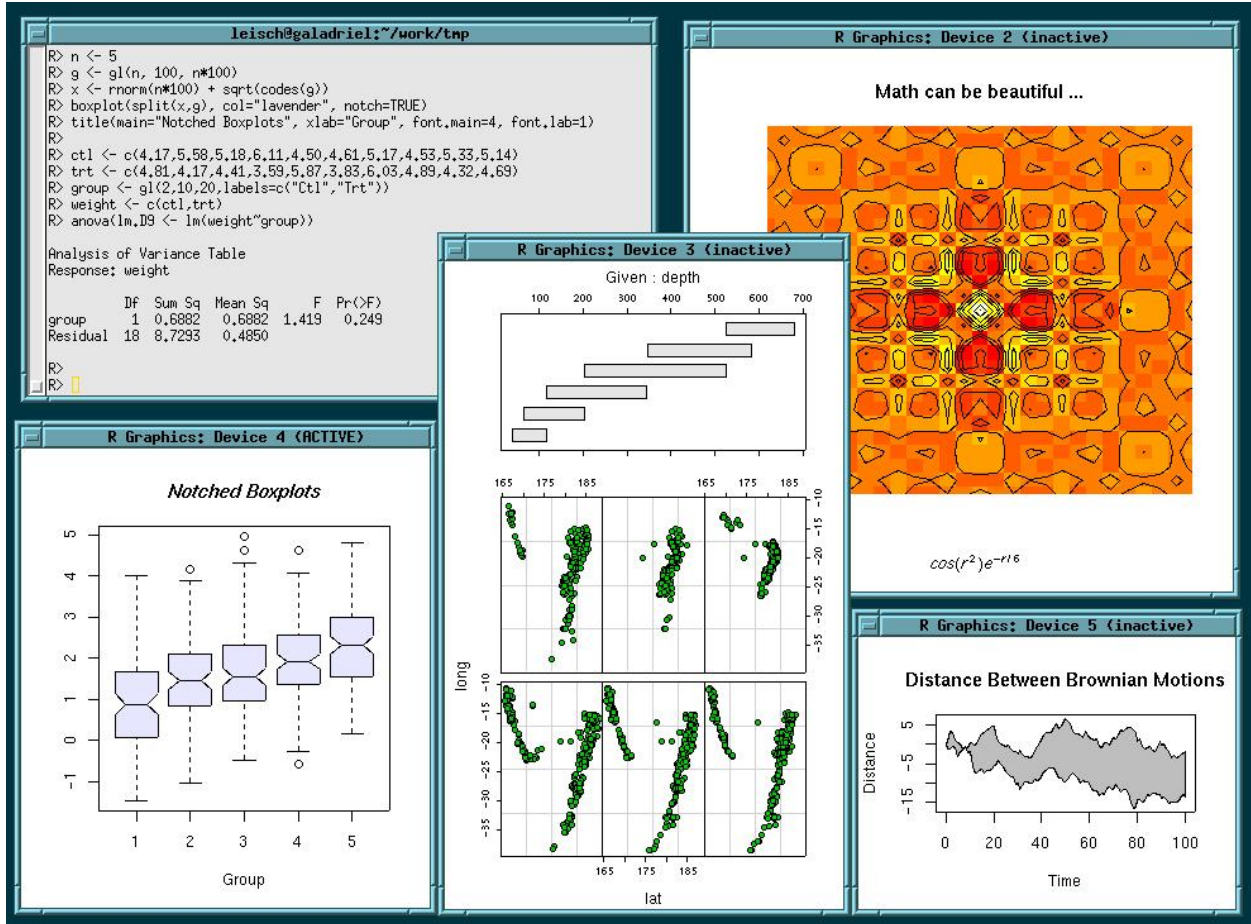


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454 Figure 1B



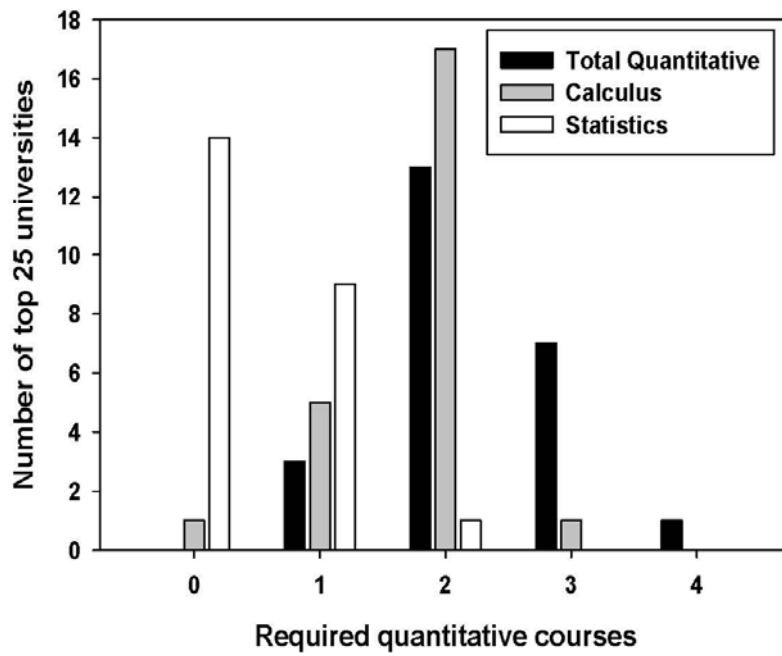
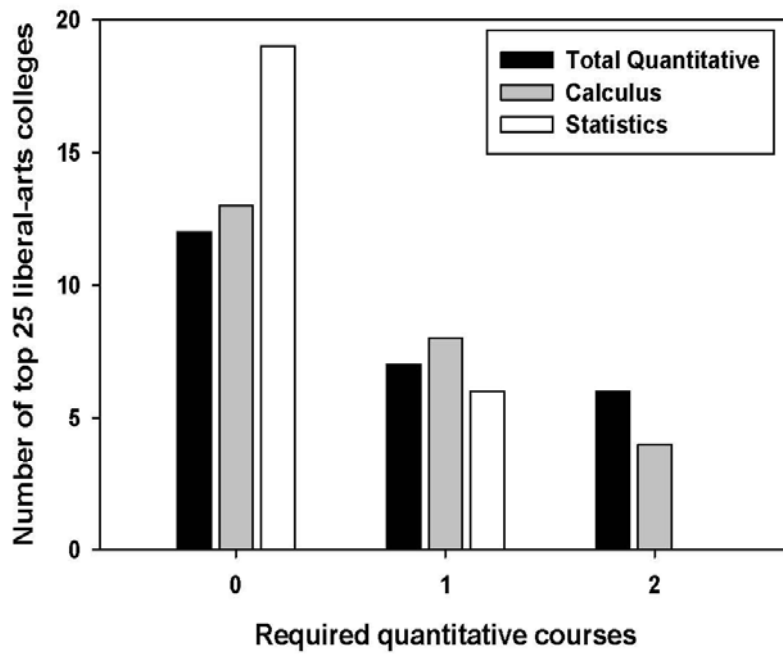
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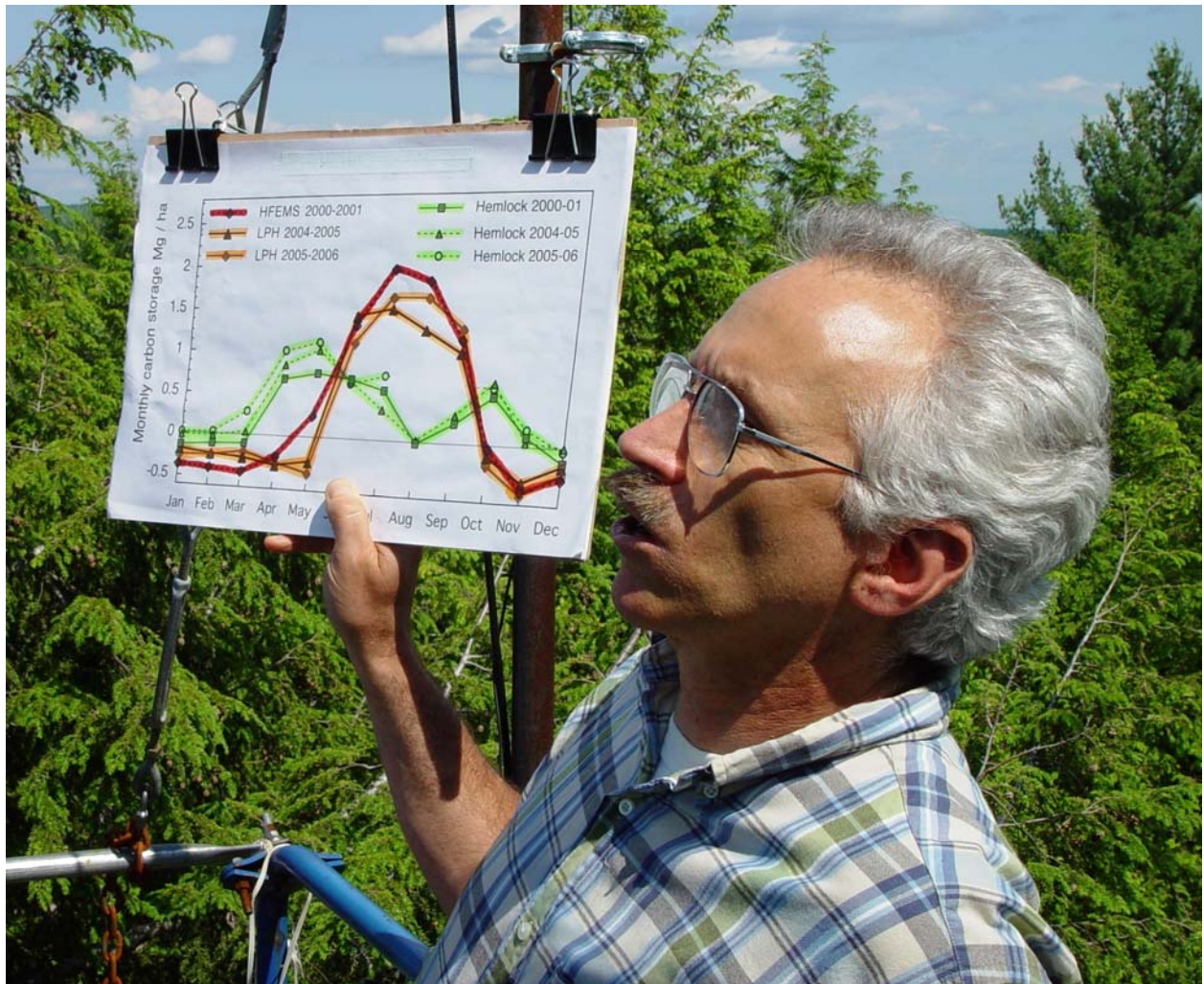
Figure 1C



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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  $\mu$  lies in the interval  
454 (10.2, 29.8) equals 0.95. But  $\mu$  is a fixed (but unknown) constant: it is either in the interval (10.2,  
455 29.8) or it is not. The probability that  $\mu$  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  $\mu$  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  $\mu$  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  $\mu$  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  $\mu$  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  $\mu$  (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  $\mu$  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.