J Insect Conserv (2007) 11:47–59
DOI 10.1007/s10841-006-9018-9

BEETLE CONSERVATION

Are we doomed to repeat history? A model of the past using tiger beetles (Coleoptera: Cicindelidae) and conservation biology to anticipate the future

David L. Pearson · Fabio Cassola

Received: 23 September 2005 / Accepted: 20 December 2005 / Published online: 7 November 2006

Abstract Studies of conservation biology involving tiger beetles have become increasingly common in the last 15 years. Governments and NGOs in several countries have considered tiger beetles in making policy decisions of national conservation efforts and have found tiger beetles useful organisms for arguing broad conservation issues. We trace the evolution of the relationship between tiger beetle studies and conservation biology and propose that this history may in itself provide a model for anticipating developments and improvements in the ability of conservation biology to find effective goals, gather appropriate data, and better communicate generalizations to non-scientific decision makers, the public, and other scientists. According to the General Continuum of Scientific Perspectives on Nature model, earliest biological studies begin with natural history and concentrate on observations in the field and specimen collecting, followed by observing and measuring in the field, manipulations in the field, observations and manipulations in the laboratory, and finally enter theoretical science including systems analysis and mathematical models. Using a balance of historical and analytical approaches, we tested the model using scientific studies of tiger beetles (Coleoptera: Cicindelidae) and the field of conservation biology. Conservation biology and tiger beetle studies follow the historical model, but the results for conservation biology also suggest a more complex model of simultaneous parallel developments. We use these results to anticipate ways to better meet goals in conservation biology, such as actively involving amateurs, avoiding exclusion of the public, and improving language and style in scientific communication.

Keywords Cicindelidae · Conservation biology · History · Models · Tiger beetles

CXLV, Studies of Tiger Beetles

D. L. Pearson (✉)
School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA
e-mail: dpearson@asu.edu

F. Cassola
Via F. Tomassucci 12/20, I-00144 Rome, Italy

Introduction

The early 20th Century Spanish philosopher, George Santayana, is credited with the quotation, "Those who cannot learn from history are doomed to repeat it." Although easily dismissed as a trivial aphorism, is it possible that this statement constitutes a testable hypothesis that we can use to understand and anticipate advances in sciences such as conservation biology?

Conservation biology is a field with too few years of experience to have engendered broad interest in its past (Zirnstein 1996; Meine 1999; Siemann 2003). However, its history together with that for longer-established supporting fields, such as systematics, genetics, wildlife management, and ecology, may hold critical information for developing future directions and goals for conservation biology. Faced with constant shortages of funding to adequately gather information and conduct studies, lessons from history may be useful as another set of tools in the quest for meeting these goals (Maienschein 2000; Gaddis 2004).

In a search for patterns within the history of scientific studies, historians have analyzed several fields from physics (Nye 1996) to biology (Killingsworth and Palmer 1992). Are there steps common to all scientific endeavor? What recognizable patterns of change take place, and what are the significant factors causing the changes? How can they best be compared? Apart from satisfying intellectual curiosity, a solid understanding of patterns in the development of science could prove useful for conservation biology in many ways. It could: (1) help determine priorities for funding agencies, (2) enable biologists to better communicate with and inform non-scientific decision makers, (3) focus individual researcher goals, (4) prepare cooperative research agendas, (5) formulate more reliable and efficient models for management and conservation goals, and (6) help anticipate problems that can then be ameliorated.

Methods

The historical model

History does not lend itself to experimental repeatability (Gould 1989), and thus tests of patterns in history rely on alternative methods. One of the most reliable techniques for answering pertinent historical questions and testing for patterns is by using insights from one field to tell us something about another—a process called consilience by historians. In so doing, we can make sense of the past and perhaps anticipate the future (Gaddis 2004). Within biology, such patterns have been proposed for understanding the historical progression of human cultures. Important causes with consistent outcomes across unrelated cultures include environmental factors (Rolett and Diamond 2004), plant and animal domestication (Diamond 2002), disease (Acemoglu et al. 2001) and food production (Hibbs and Olsson 2004).

Along the same lines, one general model of the history of science proposed to anticipate historical patterns in biology is the General Continuum of Scientific Perspectives on Nature (GCSPN) (Killingsworth and Palmer 1992). According to the GCSPN, earliest biological studies begin with natural history and concentrate on observations in the field and specimen collecting, followed by observing and measuring in the field, manipulations in the field, observations and manipulations in the laboratory, and finally enter theoretical science, including systems analysis and mathematical models. What is not clear is whether each of these chapters in the development of science can be identified as a chronological step or phase, or even more controversial, whether each step has identifiable and quantifiable characters that can be used to estimate the maturity of the field of study (Farber 2000).

In addition to these uncertainties, this model has other constraints. As with all models, simplification is an acceptable aspect of their use as long as the results are interpreted within these limitations. Also, similar to many ecological and landscape studies, using time intervals that are too small or too large can obscure important patterns. Finally, sociological, economic, and psychological forces can be more crucial in affecting models of temporal changes than generally realized, but these factors often are difficult to incorporate into general models. With these assumptions in mind, Battalio (1998) listed a series of specific characters that would demonstrate historical steps within the GCSPN model:

(STEP 1) Descriptive natural history and search for new species predominate
(STEP 2) Now an experimental science rather than a natural history model
(STEP 3) Power is transferred from expert amateurs to trained professional scientists, and graduate training for employment in the field has become available
(STEP 4) Systematics no longer dominant, and research focused more on theoretically complex issues with extensive use of graphs and statistical inference in publications
(STEP 5) Formation of research teams and increasing evidence of socialization, such as use of acknowledgments sections, associations of peers, and co-authored publications
(STEP 6) Technical terminology and methodology so refined they now limit the audience that can fully comprehend them (Fig. 1).

Test subjects

The history of entomology provides a rich and varied set of potential subjects to test the model. However,

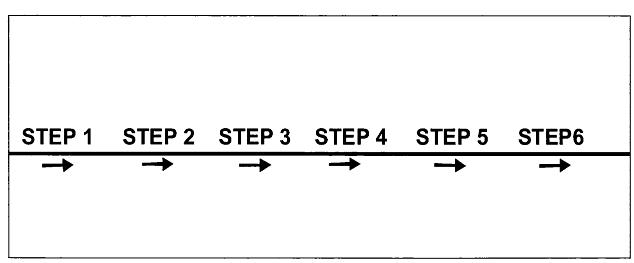

Fig. 1 Linear progression of steps in GCSPN model in which each step replaces the former one

because of the myriad and often independent histories of various insects groups within entomology (Sorensen 1995), we felt that an initial test of the GCSPN model would be more manageable by using a single group. Tiger beetles (Coleoptera: Cicindelidae) provide a relatively discrete taxonomic unit whose history is well documented (Pearson and Cassola 2005). The tiger beetles are a small but distinct group of over 2600 species whose biology is also well known (Pearson and Vogler 2001). These beetles are attractive, fast-flying and fast-running insect predators that occur in many diverse habitats around the world. Many of the same characteristics of tiger beetles that have generated considerable interest among amateurs and professional biologists have also contributed to their increasing role in conservation studies. Most important among these characteristics is the ease with which most species can be found and identified in the field, their habitat specificity, and their value as indicators of habitat health and of biodiversity. Also, because they have been well-collected and studied, their past and present distributions are known sufficiently to evaluate historic trends of decline in range or abundance (Desender et al. 1994; Knisley and Fenster 2005).

In addition, we will use the history of the field of conservation biology as a test subject. With a combination of narrative and comparative analysis, we propose to compare these two histories to test the validity of the model. Finally, we pursue the possibility that if the resultant pattern of steps conforms to the GCSPN model, can the model and its assumptions be used to anticipate and direct future steps in conservation biology?

Results

Step 1: Descriptive natural history and search for new species predominate

As claimed by the GCSPN, much of the earliest history of conservation biology revolved around documentation of species, in this case their extinctions. In the late 18th Century, American authors Ralph Waldo Emerson and Henry David Thoreau influenced the development of Transcendentalism, a philosophy associated with nature. Through their writings, preservation of nature and wilderness became a powerful, novel doctrine. In the midst of manifest destiny and impressions of inexhaustible resources, the unexpected disappearance of once abundant species, such as the Passenger Pigeon, and near extinction of the American Bison, first made extinction seem a real possibility, and the causes of extinction of individual species became an important area of study for the nascent field of conservation biology.

Because of an extensive knowledge of taxonomy and distribution starting with Linné (1758), tiger beetles lent themselves to early studies of declining populations and extinctions. As such, several species and populations of tiger beetles became some of the first insects declared legally endangered or threatened with extinction.

Pearson et al. (2005) estimate that at least 33 (15%) of the 223 named species and subspecies of tiger beetles in Canada and the United States may be declining at a rate that justifies their consideration for inclusion on the US Fish and Wildlife Service's List of Endangered and Threatened species (Fig. 2). However, at present, only four of these are officially listed by the federal government, and several others are under consideration for listing. In addition, several other countries (Belgium, Canada, Germany, Great Britain, Lithuania, The Netherlands, South Africa and Sweden), at least 24 individual states and provinces within the United States and Canada, and international NGOs (World Conservation Monitoring Centre and IUCN) have developed lists of endangered and threatened species that include tiger beetles.

Few insects are well-enough known globally to document these types of population decline. Because of the rich collections of tiger beetle specimens available for study, however, the disappearance of species from former parts of the range can be authenticated. From these historical records, some long-term changes in the environment can also be deduced (Nagano 1980; Desender and Turin 1989; Desender et al. 1994; Yarbrough and Knisley 1994; Kamoun 1996; Trautner 1996; Berglind et al. 1997; Diogo et al. 1999; Knisley and Hill 2001; Richoux 2001; Sikes 2002; Goldstein and Desalle 2003; Horgan and Chávez 2004; Mawdsley 2005). Thus, tiger beetles help offer a window into our past and can provide insight as to where protective measures are needed (Babione 2003).

Step 2: Now an experimental science rather than a natural history model

For tiger beetle studies, the major intellectual advance during the last half of the 18th Century was an often-conflicting attempt to place the growing number of species into a natural array of groupings. By moving from pure description to evolutionary questions, these attempts at phylogenetics were also some of the first signs of a change into an experimental paradigm (Barrow 1998). With more species known, better

Fig. 2 Controlled area in Santa Cruz Co., California, to protect the officially endangered Ohlone Tiger Beetle (*Cicindela ohlone*) Photo courtesy Univ. Calif. Santa Cruz Grounds Dept.

chances for comparisons, and greater competition for research subjects among the increasing number of experts, tiger beetle systematists ventured into more sophisticated areas of research. Field naturalists such as A.R. Wallace and H. W. Bates often collected tiger beetles wherever they traveled. Emergent but significant ideas about behavior, ecology and evolution also grew from their experiences of collecting and observing these beetles. The German medical doctor, Walther Horn, became the greatest authority and acknowledged specialist of the tiger beetle family, working almost solitarily for more than 50 years. Although predominantly taxonomic in nature, his articles began, later in the 1900s, to incorporate experimentally testable ideas of habitat, biogeography and intraspecific variation (subspecies).

Besides reconstructing the past, tiger beetles are useful for conservation in other ways. Because of political, sociological and economic pressures, conservation policy and research are under pressure to produce quick results. This pressure is so pervasive, and the time, money and personnel to do the work are so limited that conservation biology is called a ‘‘crisis discipline,‘‘ in which risk analysis has become a major element (Maguire 1991). A common approach to resolving these problems has been to use indicator taxa as test organisms that purportedly represent other taxa in a complex environment. By focusing studies on a small but representative subset of the habitat or ecosystem, patterns of habitat degradation and population losses can be more quickly and clearly distinguished (Noss 1990).

Unfortunately most taxa suggested for use as indicators have been selected primarily on the basis of their public appeal (Pearson 1994). The consequences have cast doubt on the general usefulness and accuracy of bioindicators in conservation policy-making. For instance, among animal taxa, most studies using indicator taxa have relied on vertebrates, especially those ‘‘species of high public interest’’ (USDI 1980). Vertebrates, however, tend to be relatively long-lived, have low rates of population increase, long generation times, and comparatively low habitat specificity (Murphy et al. 1990), all of which tax the time and finances for proper investigation. As a result, there is a trend now to rely more and more on arthropod species, especially insects, instead of, or in addition to, vertebrates as appropriate indicator taxa (Pyle et al. 1981; Kremen 1992; Samways 1994; McGeoch 1998).

Tiger beetles have been used throughout the world to test and develop better guidelines for choosing bioindicators (Holeski and Graves 1978; Schultz 1988; Bauer 1991; Pearson and Cassola 1992; Rivers-Moore and Samways 1996; Kitching 1996; Rodríguez et al. 1998; Cassola and Pearson 2000; Cassola 2002; Arndt et al. 2005). First, the category of bioindicator is determined (Kremen et al. 1993). Will it be used for monitoring (Greenberg and McGrane 1996), in inventory (Lees et al. 1999), as an umbrella (Mittermeier et al. 2004), or some other type of model organism? Then a claim is made that a species or taxon, such as tiger beetles, is ideal as a bioindicator in a specific category. That leads to tests of whether this proposed indicator taxon meets the demands of widely accepted logistical and biological criteria for ideal indicators within each category. A useful bioindicator taxon should have characteristics such as stable taxonomy, well-known biology and readily observed and manipulated (Brown 1991). More recently, it has become evident that even when chosen carefully, a single taxon is unlikely to be adequate. Seldom will a single taxon reflect accurately an entire habitat or ecosystem (Ricketts et al. 1999). Choosing a suite of indicator taxa from different trophic levels or different subhabitats within the area of interest probably produces better data on which to base rational and informed biological and policy decisions. Nevertheless, each of the suite of candidates should be vetted experimentally to determine its appropriateness for that specific use as a bioindicator.

Step 3: Power is transferred from expert amateurs to trained professional scientists, and graduate training for employment in the field has become available

In the late 1800s, the first conservation organizations, such as the Audubon Society and the Royal Society for the Protection of Birds, were formed with both professional and amateur participants. In the next few decades, the work of these professionals and amateurs created many conflicts, such as the benefits of specimen collecting and use of common names. Little by little, professional academicians and government employees with advanced degrees, such as Aldo Leopold and Rachel Carson, took over the study and communication of conservation problems. In 1985 the Society for Conservation Biology was established, and by 2000 it had 5100 professional members. Conservation studies that involve insects have become more common (Bossart and Carlton 2002) in recent years, often focused by international insect organizations, such as the Xerces Society for the Conservation of Invertebrates. In 1997 the Journal of Insect Conservation was launched in conjunction with the British Butterfly Conservation Society. By this time additional national societies dedicated to the conservation of insects had been formed in Asia, Europe and North America. Along with journals focused on this area, graduate programs and salaried positions as conservation biologists, many of whom use insects as test organisms, became established, and the leadership and predominance of professionals became more and more obvious.

For tiger beetles, the near monopoly of a single expert, Walther Horn, had great influence on the direction of studies. Beyond his tight control of tiger beetle taxonomy, however, a few other professional biologists began to publish scientific articles using tiger beetles as test organisms for geological history (Wickham 1904), ecology (Shelford 1907), and behavior (Shelford 1902). The use of tiger beetles in conservation did not begin until the late 20th Century (Pearson and Vogler 2001), and some potentially divisive problems, such as the development of common names, were less disruptive among amateur and professional tiger beetle workers (Pearson 2004) than with other groups, such as birds, butterflies and dragonflies.

Even more subtly, professionalization of scientific articles, including those for conservation biology and tiger beetle studies, is reflected in its evolving language, writing styles, and grammar. Linguistic analysis of journals and scientific articles shows consistent changes that indicate levels of expertise and establish levels of authority, further separating professionals from amateurs. Some examples of changing words include adverbs that show degrees of reliability, such as "undoubtedly" and "possibly," induction, such as "must" and "evidently," identification of hearsay evidence, such as "it seems" and "apparently," reservations of deduction, such as "presumably" and "could," and hedges, such as "approximately" (Chafe 1986). In addition, professional science writers use distinctive writing devices that include reduced use of personal pronouns, reliance on passive voice, a decrease in the number of simple sentences, the presence of technical terminology, an emphasis on reliability of evidence, and the use of citations (Lakoff and Johnson 1980). Carter (1990) also showed that although professionals rewriting scientific articles for semi-popular or popular consumption tend to write in broader generalities and use methods more similar to amateurs, they retain a concept of domain-specific knowledge that distinguishes them from the style of amateurs.

Step 4: Systematics no longer dominant, and research focused more on theoretically complex issues with extensive use of graphs and statistical inference in publications

Among tiger beetles, in areas other than taxonomy, the 1960s saw a relatively small increase in articles published on behavior, ecology, morphology, biogeography and ecology (Pearson 1988). But starting in the 1980s, physiological studies of tiger beetles emerged (Dreisig 1980; Hadley et al. 1988; Gilbert 1997; Hoback et al. 2000; Okamura and Toh 2004). In the 1990s, genetics studies began to appear (Galián et al. 1990; Proença et al. 2002), and by this time, these and other non-taxonomic publications constituted 85% of the articles on tiger beetles with statistical procedures and graphs.

One area in which tiger beetles were at the forefront of more complex conservation biology studies was in the statistical application of assumptions of dependence among data points. In initial comparisons of species patterns across regions and countries, Pearson and Cassola (1992) claimed that among the tested attributes of tiger beetles as an ideal bioindicator was a high correlation between their species numbers and those of other groups. If one goal is to establish conservation areas with the highest species diversity, tiger beetles were very useful because where you found more of them you also found more of other species like birds and butterflies. But tiger beetles, at the right season, could often be surveyed in a few weeks whereas birds took years to survey adequately in the same area. In addition, it was easy to train students and local workers to observe and sample tiger beetles, but training these same people to observe other taxa, such as birds and butterflies, was an enormous undertaking. Thus, one could argue that tiger beetles are logistically useful and biologically appropriate candidates to help represent entire habitats or ecosystems for species inventories.

A major problem, however, was the misapplication of a common simplifying component in statistical tests used by many biologists (Carroll and Pearson 1998a). In virtually all traditional statistical tests, a datum from one point in space or time is assumed to not influence or affect any another datum in the analysis obtained from a different point in space or time (independent). If, however, the data are dependent (often called autocorrelated), and many subsequent studies show that many if not most biological data are likely to be dependent, the resultant analysis may be faulty or misleading (Carroll and Pearson 2000). Many researchers now apply more appropriate statistics, such as geostatistics (Cressie 1991), in conservation biology that avoid the assumption of independence. Tiger beetles were among the first taxa using these modern analytical techniques (Carroll 1998; Pearson and Carroll 1998; 1999; Carroll and Pearson 1998b, Pearson and Carroll 2001).

In addition to pioneering statistical analyses, tiger beetles also were used in early applications of molecular analysis for geographical implications of conservation. For instance, the subdivision of lineages of the tiger beetle species, *Cicindela dorsalis*, in Florida between the Gulf of Mexico and the Atlantic Ocean, can be detected only with molecular markers. However, the fact that species of several taxa on one side of a barrier are consistently different from those on another is highly significant for conservation (Pearson and Vogler 2001). These regions of distinctive genetic overlap can reflect historical events in evolutionary time (Crandall et al. 2000; Goldstein et al. 2000; Satoh et al. 2004). By incorporating an evolutionary time scale, we not only gain another valuable factor to include in our conservation planning, but it also makes us aware that areas chosen for protection require management goals focused not just on 10, 20 or even 100 years, but for much longer into the past as well as the future (Schwartz 1999; Barraclough and Vogler 2002).

Step 5: Formation of research teams and increasing evidence of socialization, such as use of acknowledgments sections, associations of peers, and co-authored publications

Conservation biology has quickly moved from single and often isolated researchers such as Leopold and Carson to a predominance of interactive researcher teams. Among tiger beetle studies, there is considerable evidence for similar changes on a broad level, some of them apparently caused by the appearance of field guides and general books on the biology of tiger beetles beginning in the 1990s (Knisley and Schultz 1997; Leonard and Bell 1999; Acorn 2001; Choate 2003; Pearson et al. 2005; Pearson and Shetterly 2006). Before this time, only individuals with time and interest to search through often obscure journals and arcane terms could acquire the basic knowledge and identification skills to do research using tiger beetles. More specific evidence of socialization is in co-authored publications. In one of the first general reviews of tiger beetle biology (Pearson 1988), only 23% of the cited articles were co-authored. Twelve years later in a book on general tiger beetle biology (Pearson and Vogler 2001) 40% of its citations were co-authored. In 1969, an informal correspondence among tiger beetle enthusiasts developed into a journal called "Cicindela." Another indicator of socialization showed advances within this highly specialized journal. In the 1970s only 2% of its articles had acknowledgments sections; in the 1980s, 26% had these sections; and in the 1990s, 83% of them did.

Similarly, the complex nature of modern conservation biology research necessitates more and more research teams. For instance, many modern conservation biologists working on rare and endangered species now rely heavily on molecular markers (Avise 1994; Galián and Vogler 2003) to distinguish species and populations within species. The importance of conserving intra-specific variation is reflected in the U.S. Endangered Species Act, which calls for the conservation of "independent population segments". This makes conservation of distinct populations within a species a legal requirement, and involves coordination of field biologists, laboratory technicians, lawyers, and politicians. This coordination of effort is obvious in many areas of conservation biology, and recently has also become a dominant theme in tiger beetle studies (Knisley and Hill 1992; Vogler et al. 1993; Moritz 1994; Vogler and Desalle 1994; Vogler 1998).

Some promising future uses of tiger beetles have direct ramifications for conservation biology, and most of them will involve teams that are interdisciplinary. These areas include climate change (Ashworth 2001), reintroductions (Omland 2002; Brust 2002; Knisley et al. 2005), habitat reclamation (Hussein 2002), habitat management (Omland 2004) and location of conservation reserves and parks (Mittermeier and Mittermeier 1997; Desender and Bosmans 1998; Andriamampianina et al. 2000; Pearson and Carroll 2001; Mittermeier et al. 2004).

Step 6: Technical terminology and methodology so refined they now limit the audience that can fully comprehend it

Although communication with amateurs and the public is a stated goal of the developing cadre of professional conservation biologists, growing reliance on increasingly complex technology and terminology, mathematical models, sophisticated statistics and computer programs have excluded many amateurs and even some professionals in related fields.

For tiger beetles, the rapidly growing use of highly sophisticated disciplines, such as molecular biology, statistical modeling, and satellite imagery have introduced many technical words and concepts. This jargon, in turn, can quickly limit comprehension to a narrow array of associated professionals. As measured in terms of scientific discourse, this trend includes increasing length and number of published articles, increasing sentence complexity, use of multi-word noun phrases, as well as narrowly defined technical terms. It is also well advanced among tiger beetle workers, especially in complex fields, such as molecular studies (Galián et al. 1990; Morgan et al. 2000; Proença and Galián 2003; Goldstein and Desalle 2003; Pons et al. 2004) and mathematical modeling (Carroll and Pearson 2000; Van Dooren and Matthysen 2004).

Paradoxically, although the often-growing complexity of terminology and methodology used in advanced studies of tiger beetles may have excluded most amateurs and many traditional taxonomists, ecologists and behavioral researchers, it appears to have attracted others. For instance, molecular biologists and mathematical modelers seeking appropriate systems on which to apply their technology have used data from tiger beetles with little previous knowledge of the animals themselves. Also, when the U.S. Fish and Wildlife Service listed several tiger beetle species as endangered or threatened, economists, sociologists, foresters, politicians, land owners and members of many unrelated fields, who had little or no previous interest in these taxa, suddenly needed to know about them.

At this point in the march of scientific history, the exclusion of tiger beetle amateurs from complex molecular and statistical studies, while lamentable is not debilitating. However, for conservation biology, just as the field of study reaches a high level of scientific rigor that knowingly will exclude many participants, it simultaneously reaches a point where it must communicate with a growing number of essential participants. Many of these participants are unlikely to comprehend the message or be able to interpret the results of the increasingly complex but more reliable scientific effort. The legislators, judges, lawyers, teachers, and reporters who are critical for implementing policy decisions may not be able to understand the data and generalizations upon which they are basing their decisions. These apparently mutually exclusive goals and effort *are* potentially debilitating.

Discussion

Do the histories of tiger beetle studies and conservation biology follow the model?

Both tiger beetle studies and conservation biology show patterns of change over their history consistent with the GCSPN. However, conservation biology has done so at a velocity that often blurs the progression. Studies of tiger beetles took hundreds of years to arrive at Step 6 and in the last 25 years have become greatly entwined with conservation biology. Conservation biology took less than a century to reach this level, and most of the steps were passed in the last 20 years (Primack 2002).

Although the GCSPN model appears to have broad relevance as shown in its application to the brief history of conservation biology, the rapid advance of this field has apparently obscured some imperfections of the model along the way. Two significant questions need to be answered if the model is to be reliably applied to conservation biology planning.

(1) Are the steps deterministic and inevitable or are they mutable tendencies? Because the major goal of conservation biology is to protect biological diversity while providing for sustainable human needs (Primack 2002), it often seeks to change the outcome of environmental, economic and sociological trends, such as those associated with extinction and habitat destruction. If the general patterns of the GCSPN model represent tendencies that lend themselves to peremptory changes, the model can be used to anticipate problems and implement useful changes to better meet the goals of conservation biology. On the other hand, if the general patterns of the GCSPN model represent inevitable results, the changes fundamental to conservation biology goals are unlikely to be accomplished using these general steps of science development (Myers 1989; Eldredge 1998).
(2) Is each step of the model dependent on the previous step, and if so, how well-developed must a step be before the subsequent step can be initiated and developed? For instance, academic and government support for naming and revising taxa and basic studies of natural history has been in decline for decades and is unlikely to reverse course. As crisis managers, conservation biologists are often forced to make studies on taxa, natural communities and habitats that have severely incomplete foundations of knowledge, such as taxonomy and natural history (Wilson 2000; Hopkins and Freckleton 2002; Dubois 2003; Giangrande 2003). In terms of the GCSPN, the temptation is to yield to the pressures of crisis management and justify a leap from Step 1 to Step 4 or 5 with, perhaps, insufficient investment in the intermediate and supportive steps.

Such a problem evidently occurred with the development of the use of bioindicators in the 1980s and 1990s. Several conservation biologists urged that these surrogate taxa be chosen carefully with predetermined ideal characteristics for a particular use and habitat or ecosystem (Brown 1991; Pearson and Cassola 1992). Unfortunately, many subsequent articles advocating taxa as bioindicators ignored or failed to adequately justify the choice of bioindicators based on predetermined criteria such as reliable taxonomy and basic natural history knowledge. As a result, the credibility of these poorly qualified taxa was challenged, and support of the entire concept of bioindicators quickly diminished (Lawton et al. 1998; Schwartz 1999; Andelman and Fagan 2000; Dale and Beyler 2001).

In the same vein, the U.S. federal Endangered Species Act (ESA) was authorized in 1973. During its tenure, it has engendered considerable controversy, and its future is uncertain (Czech and Krausman 2001). Although property rights, conflicting economic interests, and politics have contributed to many of the controversies, testimony to U.S. congressional committees (Legislative Hearing on H.R. 2829 and H. R. 3705, 20 March 2002) by both conservation advocates and the Assistant Secretary for Fish and Wildlife and Parks place much of the blame for shortcomings of the ESA on poor scientific standards and lack of adequate independent scientific review of endangered species listings. For instance, in one official list of 36 species planned to be delisted in 1999 by then Secretary of the Interior, Bruce Babbitt, five species were already extinct by that time, four were based on taxonomic errors, and ten had been originally listed because of data errors. In this case 53% of these species should not have been on the endangered list in the first place, and a lack of scientific information was to blame (B. Babbitt, pers. com.). A powerful and sophisticated legislative policy assumed that conservation biology was at Step 4 or 5 in the GCSPN, even though Steps 1 and 2 were not sufficiently established to support an advance on to subsequent steps.

What uses does the GCSPN provide for identifying and attaining conservation biology goals?

One important role of the application of the GCSPN model to conservation biology is in providing a context so that we can focus on pertinent questions. At what points should funding agencies support specific efforts? Are there better periods than others in which to attract young recruits to maintain or increase interest in specific taxa or fields such as conservation biology? Can or should dominance by a single individual or small clique be avoided? Will professional biologists exclude the expert amateurs, or will they be able to cooperate?

A second use of the GSCPN is in recognizing broader philosophical problems. For instance, historians of science have shown how cultural differences within national or between regional organizations often dampen paradigm changes in the general area of study (Browne 1996). Can our model illuminate factors such as this and thus avoid intellectual imperialism? Can ideas and hypotheses spread quickly throughout the network, or will resistance to change and other barriers make communication ponderous? Is there a Step 7 in our GCSPN model?

Finally, these preliminary results from comparisons of tiger beetles and conservation biology highlight some specific actions that can be taken immediately. For instance in the area of communication between technical and popular audiences, a basic conservation biology goal, should or can we avoid or ameliorate Step 6?

(1) Three simple changes in writing style and editorial format could make communication easier across a spectrum of readers. First, the abstract and summary of an article can be written in a style that simplifies complex concepts for non-professionals (Gopen and Swan 1990; Knight 2003). Second, for many non-scientific readers, citations in parentheses may become a barrier that disrupts comprehension, a possibility rarely addressed or tested by scientific authors (Rudolph 2003). Using less obtrusive superscript numbers to key citations is one simple change that might broaden communication. This format is already used in several prestigious journals, such as Science, Nature and Trends in Ecology and Evolution. Third, even though metaphors are central to how we think about things, especially when explaining complex concepts to the uninitiated (Short 2000), the editors of some journals, such as Conservation Biology, explicitly discourage authors from using metaphors. Encouraging the use of suitable metaphors to enhance communication might prove more appropriate (Chew and Laubichler 2003).

(2) Although administrators and professional colleagues may demand publications in peer-reviewed journals for promotion and tenure, less prestigious methods for communicating results to the public, such as newspaper and magazine articles, books, and web sites, must receive more than a tacit blessing.

(3) Even though most professional conservation biologists lack the talent or time to communicate with the public as well as Rachel Carson, Jared Diamond, Aldo Leopold, or E.O. Wilson, there are talented science writers, such as David Quamen, Jonathan Weiner and Peter Matthiessen, who can make complex scientific writing comprehensible and attractive to a wide range of the public who have little or no science background. Cooperating with these types of writers, even though credit may be diluted, could disseminate critical information effectively to a wider audience.

(4) Descriptions of new species of tiger beetles, natural history observations, geographical distributions, and seasonal records of occurrence and dispersion, as in many taxa, have by default been turned over largely to expert amateurs. However, not all professionals accept the resultant data as reliable. Recently the British social critics, Charles Leadbeater and Paul Miller (2004), identified a rapidly-growing involvement of amateurs in science from astronomy to medicine that is not fully recognized or utilized. These investigators are a new breed of largely self-trained experts or professional amateurs (Pro-Ams) who, using modern technology, such as the Internet, are producing significant innovations and discoveries in a wide range of fields. Both the government and professionals need to facilitate the contributions of Pro-Ams and be prepared to share the stage with them.

Conclusions

As is typical of model-testing, results often reveal exceptions, unforeseen data, and other anomalies. One accepted procedure in the face of such problems, is to incorporate these unexpected results into a more generalized and useful model. From results of our preliminary consilience tests of the GCSPN, several changes are evident that would make the model more useful. For instance, the history of tiger beetles shows that productive researchers can be working simultaneously in several if not all the steps, especially at later times in the history of a scientific field. Thus it might be more accurate to consider the steps as benchmarks in a continuum rather than linear chronological progressions or irreversible advances. Also, even within well-defined taxa, amateur and professional lines of change appear to diverge into parallel lines rather than follow a single evolving line of science used in the original model (Battalio 1998) (Fig. 1). These parallel lines often have cross lines of influence and varying levels of communication. The different lines each may have their own characteristic benchmarks (Fig. 3). It is also obvious that broader fields, such as conservation biology, build on the work of contributing areas of interest and incorporate their histories rather than follow an independent disciplinary track. Thus, in these succeeding fields, the velocity of change along the time continuum could be expected to be faster and with entire groups of lines converging.

To better understand the model, future tests are needed to clarify not only its patterns but the causes of the patterns. Consilience comparisons of the history of additional taxa or disciplines are one obvious approach. Do all taxa and fields follow the same sequence of steps? Do some histories reveal accelerated progress through certain steps and not others? Accumulated similarities and differences among these histories will provide opportunities to look for their causes. Do factors such as species numbers, their conspicuousness, economic importance, number of investigators, and level of research funding influence patterns and advances in the progression of steps within a field? With an understanding of various combinations of characteristics that might cause differences in development or speed of change, we would be in a better position to understand and apply the model. Among insects, taxa such as ants, cerambycid beetles, scarab beetles, butterflies, dragonflies, and termites would be good candidates for test organisms (New 1984; 1991; 1998; Gaston et al. 1993; Samways 1994; 2005). Comparisons of the history of fields such as wildlife biology, population genetics, and landscape ecology could also be enlightening.

With some immediate solutions and the promise of even more important long range solutions made possible by examinations of historical models, such as the GCSPN, we can be encouraged that conservation biology can make use of its history and learn from it. For instance, Leadbeater and Miller's thesis indicates that with conscious effort the diverging model in Fig. 3

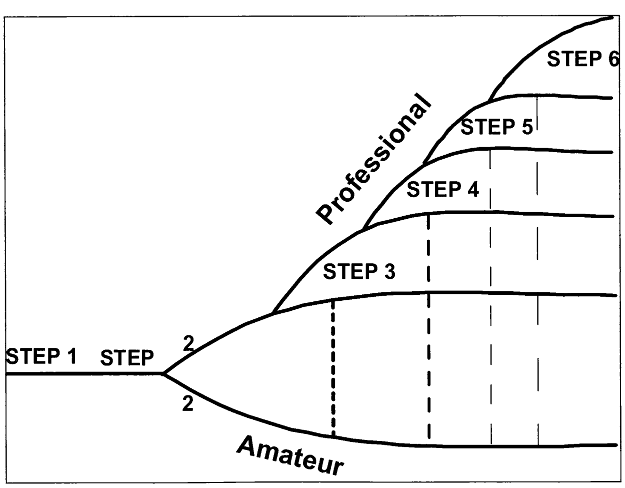

Fig. 3 More complex relation of steps in the GCSPN model as suggested by assessment of the history of tiger beetle studies and conservation biology. Vertical dashed lines indicate varying degrees of communication between amateurs and professionals in the progression

might morph eventually into a model with converging lines, at least between amateurs and early steps in the professional progression of changes. With improvements in the model and future tests of the process of science itself, we may have the best chance to develop foresight, learn from history, and better know if and what changes can be made to better reach our goals. We need not be doomed to repeat history, and even more positively, it may well be that, ''We know the future only by the past we project into it'' (Gaddis 2004).

Acknowledgements We are indebted to J. Alcock, K.R. Johnson, C.B. Knisley, B.A. Minteer, N.B. Pearson, S.J. Pyne and D. Sikes for reading early drafts of this manuscript and providing helpful criticism to improve it. J.H. Acorn first challenged us to think about some of these problems and solutions.

References

Acemoglu D, Johnson S, Robinson JA (2001) The colonial origins of comparative development: an empirical investigation. Am Econ Rev 91:1369–1401

Acorn JH (2001) Tiger beetles of Alberta: killers on the clay, stalkers on the sand. Univ. of Alberta Press, Edmonton, Alberta

Andelman SJ, Fagan WF (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? PNAS 97:5954–5959

Andriamampianina L, Kremen C, Vane-Wright D, Lees D, Razafimahatratra V (2000) Taxic richness patterns and conservation evaluation of Madagascan tiger beetles (Coleoptera: Cicindelidae). J Insect Cons 4:109–128

Arndt E, Aydin N, Aydin G (2005) Tourism impairs tiger beetle (Cicindelidae) populations—a case study in a Mediterranean beach habitat. J Insect Cons 9:201–206

Ashworth AC (2001) Chp. 8: perspectives on quaternary beetles and climate change. In: Gerhard LC, Harrison BM (eds) Geological perspectives of global climate change. American Association of Petroleum Geologists Studies in Geology #47, Tulsa, Oklahoma, pp 153–168

Avise JC (1994) Molecular markers, natural history and evolution. Chapman and Hall, New York

Babione M (2003) Bringing tiger beetles together. Endangered Species Bull 28:28–29

Barraclough TG, Vogler AP (2002) Recent diversification rates in North American tiger beetles estimated from a dated mtDNA phylogenetic tree. Mol Biol Evol 19:1706–1716

Barrow MV Jr (1998) A passion for birds: American ornithology after Audubon. Princeton University Press, Princeton, New Jersey

Battalio JT (1998) The rhetoric of science in the evolution of American ornithological phases. ATTW contemporary studies in technical communication, vol. 8. Ablex Publishing Corporation, Stamford, Connecticut

Bauer KL (1991) Observations on the developmental biology of *Cicindela arenicola* Rumpp (Coleoptera, Cicindelidae). Great Basin Nat 51:226–235

Berglind S-A, Ehnström B, Ljungberg H (1997) Strandskalbaggar, biologisk mångfald och reglering av små vattendrag—exemplen Svartån och Mjällån. Entomologisu Tidskrift 118:137–154

Bossart JL, Carlton CE (2002) Insect conservation in America: status and perspectives. Am Entomol 48:82–92
Brown KS Jr (1991) Conservation of neotropical environments: insects as indicators. In: Collins NM, Thomas JA (eds) Conservation of Insects and their Habitats. Academic Press, London, United Kingdom, pp 349–404
Browne J (1996) Biogeography and empire. In: Jardine N, Secord JA, Spary EC (eds) Cultures of natural history. Cambridge Univ. Press, Cambridge, United Kingdom, pp 305–321
Brust ML (2002) Reintroduction study on *Cicindela formosa generosa* in Marinette County, Wisconsin. Cicindela 34:5–7
Carroll SS (1998) Modelling abiotic indicators when obtaining spatial predictions of species richness. Environ Ecol Stat 5:257–276
Carroll SS, Pearson DL (1998a) Spatial modeling of butterfly species richness using tiger beetles (Cicindelidae) as a bioindicator taxon. Ecol Appl 8:531–543
Carroll SS, Pearson DL (1998b) The effects of scale and sample size on the accuracy of spatial predictions of tiger beetle (Cicindelidae) species richness. Ecography 21:401–414
Carroll SS, Pearson DL (2000) Detecting and modeling spatial and temporal dependence in conservation biology. Cons Biol 14:1893–1897
Carter M (1990) The idea of expertise: an exploration of cognitive and social dimensions of writing. College Compos Commun 41:265–286
Cassola F (2002) Le cicindele e le coste: biogeografia e conservazione (Studi sui Cicindelidi. CXIX). Biogeographia 23:55–69
Cassola F, Pearson DL (2000) Global patterns of tiger beetle species richness (Coleoptera: Cicindelidae): their use in conservation planning. Biol Cons 95:197–208
Chafe W (1986) Evidentiality in English conversation and academic writing. In: Chafe W, Nichols J (eds) Evidentiality: the linguistic coding of epistemology. Albex Press, Norwood, NJ, pp 261–272
Chew MK, Laubichler MD (2003) Natural enemies: metaphor or misconception? Science 301:52–53
Choate PM (2003) Tiger beetles: a field guide and identification manual for Florida and Eastern US. Univ. Press of Florida, Gainesville, Florida
Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK (2000) Considering evolutionary processes in conservation biology. Trends Ecol Evol 15:290–295
Cressie N (1991) Statistics for spatial data. John Wiley, New York, NY
Czech B, Krausman PR (2001) The endangered species act: history, conservation biology, and public policy. Johns Hopkins Univ. Press, Baltimore, Maryland
Dale VH, Beyler SC (2001) Challenges in the development and use of ecological indicators. Ecol Indicators 1:3–10
Desender K, Bosmans R (1998) Ground beetles (Coleoptera, Carabidae) on set-aside fields in the Campine region and their importance for nature conservation in Flanders (Belgium). Biodivers Conserv 7:1485–1493
Desender K, Dufrêne M, Maelfait J-P (1994) Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a data base covering more than a century. In: Desender K et al. (eds) Carabid beetles: ecology and evolution. Kulwer Academic Publishers, Netherlands, pp 247–252
Desender K, Turin H (1989) Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four west European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). Biol Cons 48:277–294
Diamond J (2002) Evolution, consequences and future of plant and animal domestication. Nature 418:700–707
Diogo AC, Vogler AP, Gimenez A, Gallego D, Galián J (1999) Conservation genetics of *Cicindela deserticoloides*, an endangered tiger beetle endemic to southeastern Spain. J Insect Cons 3:117–123
Dreisig H (1980) Daily activity, thermoregulation and water loss in the tiger beetle *Cicindela hybrida*. Oecologia 44:376–389
Dubois A (2003) The relationships between taxonomy and conservation biology in the century of extinctions. Comptes Rendus Biologies 326(supplement):9–21
Eldredge N (1998) Life in the balance. Humanity and the biodiversity crisis. Princeton Univ. Press, Princeton, NJ
Farber PL (2000) Finding order in nature: The naturalist's tradition from Linnaeus to E.O. Wilson. Johns Hopkins University Press, Baltimore Maryland
Gaddis JL (2004) The landscape of history: how historians map the past. Oxford Univ. Press, New York, New York
Galián J, Vogler AP (2003) Evolutionary dynamics of a satellite DNA in the tiger beetle species pair *Cicindela campestris* and *C. maroccana*. Genome 46:213–223
Galián J, Serrano J, Ortiz AS (1990) Karyotypes of nine species of Cicindelini and cytotaxonomic notes on Cicindelinae (Coleoptera, Carabidae). Genetica 82:17–24
Gaston KJ, New TR, Samways MJ (1993) Perspectives on insect conservation. Intercept Publ., Andover, Hants, UK
Giangrande A (2003) Biodiversity, conservation, and the "taxonomic impediment." Aquat Conserv-Marine Freshwater Ecosys 13:451–459
Gilbert C (1997) Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae). J Comp Physiol A 181:217–230
Goldstein PZ, Desalle R (2003) Calibrating phylogenetic species formation in a threatened insect using DNA from historical specimens. Mol Ecol 12:1993–1998
Goldstein PZ, Desalle R, Amato G, Vogler AP (2000) Conservation genetics at the species boundary. Cons Biol 14:120–131
Gopen GD, Swan JA (1990) The science of scientific writing. Am Sci 78:550–558
Gould SJ (1989) Wonderful life: the burgess shale and the nature of history. Norton, New York, New York
Greenberg CH, McGrane A (1996) A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. Forest Ecol Manag 89:31–41
Hadley NF, Schultz TD, Savill A (1988) Spectral reflectances of three tiger beetle subspecies (*Neocicindela perhispida*): correlation with their habitat substrate. NZ J Zool 15: 343–346
Hibbs DA, Olsson O (2004) Geography, biogeography, and why some countries are rich and others are poor. PNAS USA 101:3715–3720
Hoback WW, Podrabsky JE, Higley LG, Stanley DW, Hand SC (2000) Anoxia tolerance of con-familial tiger beetle larvae is associated with differences in energy flow and anaerobiosis. J Comp Physiol B 170:307–314
Holeski PM, Graves RC (1978) An analysis of the shore beetle communities of some channelized streams in northwest Ohio (Coleoptera). Great Lakes Entomol 11:23–36
Hopkins GW, Freckleton RP (2002) Declines in the numbers of amateur and professional taxonomists: implications for conservation. Anim Conserv 5:245–249
Horgan FG, Chávez JC (2004) Field boundaries restrict dispersal of a tropical tiger beetle, *Megacephala angustata* Chevrolet 1841 (Coleoptera: Cicindelidae). Entomotropica 19:147–152

Hussein ML-a (2002) Ground beetle (Coleoptera, Carabidae) communities of the exhausted open-cast mining area K^{TM}nigsaue and of agricultural areas in the District Aschersleben-sta§furt (Saxony-Anhalt). Arch Phytopathol Plant Protect 35:125–155
Kamoun S (1996) Occurrence of the threatened *Cicindela senilis frosti* Varas Arangua in an inland salt marsh in Riverside County, California (Coleoptera: Cicindelidae). Coleop Bull 50:369–371
Killingsworth MJ, Palmer JS (1992) Ecospeak: rhetoric and environmental politics in America. So. Illinois Univ. Press, Carbondale, Illinois
Kitching IJ (1996) Identifying complementary areas for conservation in Thailand: an example using owls, hawkmoths and tiger beetles. Biodivers Conserv 5:841–858
Knight J (2003) Scientific literacy: clear as mud. Nature 423: 376–378
Knisley CB, Fenster MS (2005) Apparent extinction of the tiger beetle, *Cicindela hirticollis abrupta* (Coleoptera: Carabidae: Cicindelinae). Coleop Bull 59:451–458
Knisley CB, Hill JM (1992) Effects of habitat change from ecological succession and human impact on tiger beetles. Virginia J Sci 43:134–142
Knisley CB, Hill JM (2001) Biology and conservation of the coral pink sand dunes tiger beetle, *Cicindela limbata albissima*. West N Am Nat 61:381–394
Knisley CB, Hill JM, Scherer AM (2005) Translocation of threatened tiger beetle *Cicindela dorsalis dorsalis* (Coleoptera: Cicindelidae) to Sandy Hook, New Jersey. Ann Ent Soc Am 98:552–557
Knisley CB, Schultz TD (1997) The biology of tiger beetles and a guide to the species of the South Atlantic States. Virginia Mus Nat Hist, Special Publication No. 5, Martinsville, Virginia
Kremen C (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. Ecol Appl 2: 203–217
Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: their use as indicators in conservation planning. Cons Biol 7:796–808
Lakoff G, Johnson M (1980) Metaphors we live by. Univ. Chicago Press, Chicago, Illinois
Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodd M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity in inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76
Leadbeater C, Miller P (2004) The pro-Am revolution: how enthusiasts are changing our economy and society. Demos Publ., London, United Kingdom
Lees DC, Kremen C, Andriamampianina L (1999) A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. Biol J Linn Soc 67:529–584
Leonard JG, Bell RT (1999) Northeastern tiger beetles: a field guide to tiger beetles of New England and Eastern Canada. CRC Press, Boca Raton, Florida
Linné Kv (1758) Systema naturae, ed. 10 (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata). Holmiae
Maguire LA (1991) Risk analysis for conservation biologists. Cons Biol 5:123–125
Mawdsley JR (2005) Extirpation of a population of *Cicindela patruela* Dejean (Coleoptera: Carabidae: Cicindelini) in suburban Washington, DC, USA. Proc Entomol Soc Wash 107:64–70
Maienschein J (2000) Why study history for science? Biol Philos 15:339–348
McGeoch MA (1998) The selection, testing and application of terrestrial insects as bioindicators. Biol Rev 73:181–201
Meine C (1999) It's about time: conservation biology and history. Cons Biol 13:1–3
Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca G (2004) Hotspots revisted: earth's biologically richest and most endangered terrestrial ecosystems. CEMEX, Mexico City, Mexico
Mittermeier R, Mittermeier CG (1997) Megadiversity: earth's biologically wealthiest nations. CEMEX, Mexico City, Mexico
Morgan M, Knisley CB, Vogler AP (2000) New taxonomic status of the endangered tiger beetle *Cicindela limbata albissima* (Coleoptera: Cicindelidae): evidence from mtDNA. Ann Entomol Soc Am 93:1108–1115
Moritz C, (1994) Defining ''Evolutionary Significant Units'' for conservation. Trends Ecol Evol 9:373–375
Murphy DD, Freas KE, Weiss SB (1990) An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Cons Biol 4:41–51
Myers N (1989) A major extinction spasm: predictable and inevitable? In: Western D, Pearl MC (eds) Conservation for the twenty-first century. Oxford Univ. Press, Oxford, United Kingdom, pp 42–49
Nagano CD (1980) Population status of the tiger beetles of the genus *Cicindela* (Coleoptera: Cicindelidae) inhabiting the marine shoreline of Southern California. Atala 8:33–42
New TR (1984) Insect conservation: an australian perspective. Dordrecht Publ., Hingham, Massachusetts
New TR (1991) Butterfly conservation. Oxford Univ. Press, Oxford, UK
New TR (1998) Invertebrate surveys for conservation. Oxford Univ. Press, Oxford, UK
Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Cons Biol 4:355–364
Nye MJ (1996) Before big science: the pursuit of modern chemistry and physics, 1800–1940. Twayne Publishers, New York, New York
Okamura J-Y, Toh Y (2004) Morphological and physiological identification of medulla interneurons in the visual system of the tiger beetle larva. J Comp Physiol A 190:449–468
Omland KS (2002) Larval habitat and reintroduction site selection for *Cicindela puritana* in Connecticut. Northeastern Nat 9:433–450
Omland KS (2004) Puritan tiger beetle (*Cicindela puritana*) on the Connecticut River: habitat management and translocation alternatives. In: Akçakaya HR, Burgman MA, Kindvall O, Wood CC, Sjögren-Gulve P, Hatfield JS, McCarthy MA (eds) Species conservation and management: case studies. Oxford Univ. Press, London, pp 137–148
Pearson DL (1994) Selecting indicator taxa for the quantitative assessment of biodiversity. Philos Trans R Soc Lond B 345:75–79
Pearson DL (1988) Biology of tiger beetles. Ann Rev Entomol 33:123–147
Pearson DL (2004) A list of suggested common English names for species of tiger beetles (Coleoptera: Cicindelidae) occurring in Canada and the US. Cicindela 36:31–39

Pearson DL, Carroll SS (1998) Global patterns of species richness: spatial models for conservation planning using bioindicators and precipitation. Cons Biol 12:809–821
Pearson DL, Carroll SS (1999) The influence of spatial scale on cross-taxon congruence patterns and prediction accuracy of species richness. J Biogeog 26:1079–1090
Pearson DL, Carroll SS (2001) Predicting patterns of tiger beetle (Coleoptera: Cicindelidae) species richness in northwestern South America. Stud Neotrop Fauna Environ 36:123–134
Pearson DL, Cassola F (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Cons Biol 6:376–391
Pearson DL, Cassola F (2005) A quantitative analysis of species descriptions of tiger beetles (Coleoptera: Cicindelidae), from 1758 to 2004, and notes about related developments in biodiversity studies. Coleop Bull 59:184–193
Pearson DL, Knisley CB, Kazilek CJ (2005) A field guide to the tiger beetles of the United States and Canada: identification, natural history and distribution of the cicindelids. Oxford Univ. Press, New York, New York
Pearson DL, Shetterly JA (2006) How do published field guides influence interactions between amateurs and professionals in entomology? Am Entomol 52. In press
Pearson DL, Vogler AP (2001) Tiger beetles: the evolution, ecology and diversity of the cicindelids. Cornell Univ. Press, Ithaca, New York
Pons J, Barraclough TG, Theodorides K, Cardoso A, Vogler AP (2004) Using exon and intron sequences of the gene Mp20 to resolve basal relationships in *Cicindela* (Coleoptera: Cicindelidae). Syst Biol 53:554–570
Primack RB (2002) Essentials of conservation biology, 3rd edn. Sinauer Associates, Sunderland, Massachusetts
Proença SJR, Galián J (2003) Chromosome evolution in the genus *Cicindela*: physical mapping and activity of rDNA loci in the tiger beetle species *Cicindela littoralis* and *C. flexuosa*. J Zool Syst Evol Res 41:227–232
Proença SJR, Serrano ARM, Collares-Pereira J (2002) An unusual karyotype with low chromosome number in Megacephalini, a basal group of tiger beetles (Coleoptera, Cicindelidae): cytogenetic characterisation by C-banding and location of rDNA genes. Hereditas 137:202–207
Pyle R, Bentzien M, Opler P (1981) Insect conservation. Ann Rev Entomol 26:233–258
Richoux P (2001) Sensibilité de *Cylindera arenaria* aux aménagements fluviaux: l'example de la région lyonnaise (Coléptères Cicindelidae). Cahiers scientifique Mus.d'Histoire nat. Lyon 2:63–74
Ricketts TH, Dinerstein E, Olson DM, Loucks C (1999) Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. Bioscience 49:369–381
Rivers-Moore NA, Samways MJ (1996) Game and cattle tramping, and impacts of human dwellings on arthropods at a game park boundary. Biodivers Conserv 5:1545–1556
Rodríguez JP, Pearson DL, Barrera RR (1998) A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? Biol Cons 83:69–76
Rolett B, Diamond J (2004) Environmental predictors of pre-European deforestation on Pacific Islands. Nature 431: 443–446
Rudolph VJ (2003) Modifying forest management for biodiversity. Cons Biol 17:1463–1571
Samways MJ (1994) Insect conservation biology. Chapman and Hall, London, UK
Samways MJ (2005) Insect diversity conservation. Cambridge Univ. Press, Cambridge, UK
Satoh A, Sota T, Uéda T, Enokido Y, Paik§ C, Hori M (2004) Evolutionary history of coastal tiger beetles in Japan based on a comparative phylogeography of four species. Mol Ecol 13:3057–3069
Schultz TD (1988) Destructive effects of off-road vehicles on tiger beetle habitat in central Arizona. Cicindela 20:25–29
Schwartz MW (1999) Choosing the appropriate scale of reserves for conservation. Ann Rev Ecol Syst 30:83–108
Shelford R (1902) Observations on some mimetic insects and spiders from Borneo and Singapore. Proc Zool Soc London 1902:230–284
Shelford VE (1907) Preliminary note on the distribution of the tiger beetles (*Cicindela*) and its relation to plant succession. Biol Bull Marine Biol Lab, Woods Hole 14:9–14
Short DC (2000) Analysing metaphor in human resource development. Human Resour Devel Int 3:323–341
Siemann W (eds) (2003) Umweltgeschichte: Themen und Perspektiven. Verlag C. H. Beck oHG, Munich, Germany
Sikes DS (2002) Beetles of Block Island: rare species that once occurred on the mainland, Chapter 11. In: Paton PW, Gould LL, August PV, Frost AO (eds) The ecology of Block Island: proceedings of the Rhode Island natural history survey conference, October 28, 2000. Rhode Island Natural History Survey, Kingston, RI, pp 183–191
Sorensen WC (1995) Brethren of the net: American entomology 1840–1880. Univ. of Alabama Press, Tuscaloosa, Alabama
Trautner J (1996) Historische und aktuelle Bestandssituation des Sandlaufkäfers *Cicindela arenaria* Fuesslin, 1775 in Deutschland (Col., Cicindelidae). Entomol Nact Berichte 40: 83–88
USDI (1980) Habitat evaluation procedures (HEP). Ecological services manual number 102. Division of Ecological Services, USDI. Fish and Wildlife Service, Washington, DC
Van Dooren TJM, Matthysen E (2004) Generalized linear models for means and variances applied to movements of tiger beetles along corridor roads. J Anim Ecol 73: 261–271
Vogler AP, Knisley CB, Glueck SB, Hill JM, Desalle R (1993) Using molecular and ecological data to diagnose endangered populations of the Puritan Tiger Beetle *Cicindela puritana*. Mol Ecol 2:375–383
Vogler AP (1998) Extinction and the evolutionary process in endangered species: what to conserve? In: DeSalle R, Schierwater B (eds) Molecular approaches to ecology and evolution. Birkhäuser Verlag, Basel, Switzerland, pp 191–210
Vogler AP, DeSalle R (1994) Diagnosing units of conservation management. Cons Biol 8:354–363
Wickham HF (1904) The influence of the mutations of the Pleistocene lakes upon the present distribution of *Cicindela*. Am. Nat. 38:643–654
Wilson EO (2000) On the future of conservation biology. Cons Biol 14:1–3
Yarbrough WW, Knisley CB (1994) Distribution and abundance of the coastal tiger beetle, *Cicindela dorsalis media* (Coleoptera: Cicindelidae), in South Carolina. Ent News 105: 189–194
Zirnstein G (1996) Ökologie und Umwelt in der Geschichte. Ökologie und Wirtschaftforschung, Band 14. Metropolis-Verlag, Marburg, Germany