

The Legacy of Extinction Risk

LESSONS FROM GIANT PANDAS AND OTHER THREATENED CARNIVORES

John L. Gittleman & Andrea J. Webster

ALL SPECIES ultimately go extinct. Currently, over 1100 mammal species (~25%) are threatened with the likelihood of extinction (Hilton-Taylor 2000). As extinction is a fundamental evolutionary process, not all of these species will survive. Today, however, the pattern and process of extinction is clearly different than in the geological past, as anthropogenic factors have become increasingly and distressingly influential. The risk of extinction now is a dual process of species' biological characteristics adapting to extreme human effects of habitat loss, overexploitation, invasives, and other secondary "chains of extinction" (Diamond 1989). A primary task for conservation biology is to better understand this dual connection, such that there develops a more proactive science, not merely reacting to forces of species decline but establishing preventive measures to stem the likelihood of greater numbers of extinctions. To do this, we must utilize as many approaches as possible, including some that seem tangential to the goals and action of conservation.

In this chapter, we consider how phylogenies or evolutionary trees can lend insight into what biological characteristics contribute to extinction

risk. Specifically, we use the recent advent of "supertrees" (see Bininda-Emonds, chapter 1), complete phylogenies based on all molecular and morphological data available for a taxon, to present some evolutionary patterns of what traits extinction-prone species in the order Carnivora have in common. We then examine whether the traits that are correlated with endangered status in general are also found in the giant panda (*Ailuropoda melanoleuca*). Our view is that these types of comparative results can be useful in two prescriptive ways. One is that by taking a broad, comparative approach, closely related (sister) taxa may help to inform us about poorly known species. The second is that, for such species as the giant panda, which we know (unfortunately) to be threatened, we can more carefully study, monitor, and preserve the precise biological characteristics of species that are declining.

SUPERTREES: APPLICATIONS TO CONSERVATION

From historical uses, such as Darwin's presentation of only one figure illustration (a phylogeny) in the *Origin*, or Haeckel's demonstration that

ontogeny recapitulates phylogeny, to modern uses regarding the history of life or the origin of acquired immune deficiency syndrome (AIDS), the promise of phylogenies in biology is tremendous (Harvey et al. 1996; Hillis 1997; O'Brien et al. 2001). Today, in conservation, phylogenies are increasingly being used for a variety of problems ranging from the identification of taxa that have high speciation and extinction rates (Barracough et al. 1999) to the preservation of evolutionary history residing in biodiversity hotspots (Sechrest et al. 2002) to selection criteria for measuring losses of biodiversity (Vizques and Gittleman 1998; Purvis and Hector 2000). The frustration has always been that the number of available phylogenies for many taxa is low and agreement among them contentious. To some degree, these problems have been assuaged, at least to the point that applications of phylogenies outweigh the negatives. Now, more phylogenies are available than ever, with over 16,000 papers published in the past thirty years on mammals alone (Liu et al. 2001). Congruence among phylogenies is, and will always be, more problematic; disagreements among molecular and morphological evidence, which taxa should be included due to questions of monophyly, or algorithms for discriminating among alternative phylogenies are important issues to resolve in systematics.

A recent development has permitted a way around these problems, so that phylogenetic information, although not perfect, can be used. These are "supertrees" (for a review, see Bininda-Emonds et al. [2002]). Any complete phylogeny that contains all species from a combination of phylogenies is a supertree. The basic idea is that the supertree provides a thorough collection of phylogenies for a given (monophyletic) group. This collection is then placed in a large matrix constructed from a simple set of rules, whereby each taxon in a clade is related and those not in the clade are unrelated (Sanderson et al. 1998). Parsimony is applied to the matrix to form a complete tree. Obviously, as in any phylogenetic reconstruction, there are various ways of assembling the details of a supertree. For example,

some are dependent on preferred character information (e.g., molecular rather than morphological), particular algorithms for combining independent trees, or the use of phylogenies that are in agreement (Baum 1992; Ragan 1992; Sanderson et al. 1998; Springer and de Jong 2001). Significantly, recent work shows that, for some groups (e.g., carnivores), there is actually remarkably good agreement among different types of characters (Bininda-Emonds 2000) and variations in the algorithms used to reconstruct supertrees seem to have only minor effects, given that there is relative congruence among the original source trees (Purvis and Webster 1999; Bininda-Emonds and Sanderson 2001).

At present, supertrees have been assembled for primates (Purvis, 1995), carnivores (Bininda-Emonds et al. 1999), bats (Jones et al. 2002) and, at the family level, all eutherian orders (Liu et al. 2001). The one employed here is for the carnivores, which is a complete tree for all 271 species of Carnivora (figure 16.1; see also Bininda-Emonds, chapter 1). It is derived from 166 phylogenies, with the overall supertree being fairly well resolved. Indeed, with respect to the giant panda and other ursids, the percentage resolution is 85.7% among twenty-eight source trees and the number of elements per tree is the third highest among the ten major carnivore families.

The critical feature of using the carnivore supertree in the present context is that a complete species-level phylogeny permits large-scale evolutionary studies about extinction risk that otherwise could not be performed (Purvis 1996; Gittleman 2001). Extinction occurs over time periods that are beyond population-level analyses. Furthermore, at least twenty-four biological traits have been identified with processes of extinction (McKinney 1997) which means that to have any meaningful analyses of the factors related to extinction in a given taxon, it is necessary to carry out tests across multiple taxa that have evolved independently. In addition, once we have identified correlates of extinction risk, it then would be helpful if we could better understand how these traits are evolving. For example, if we detect that small litter sizes and long

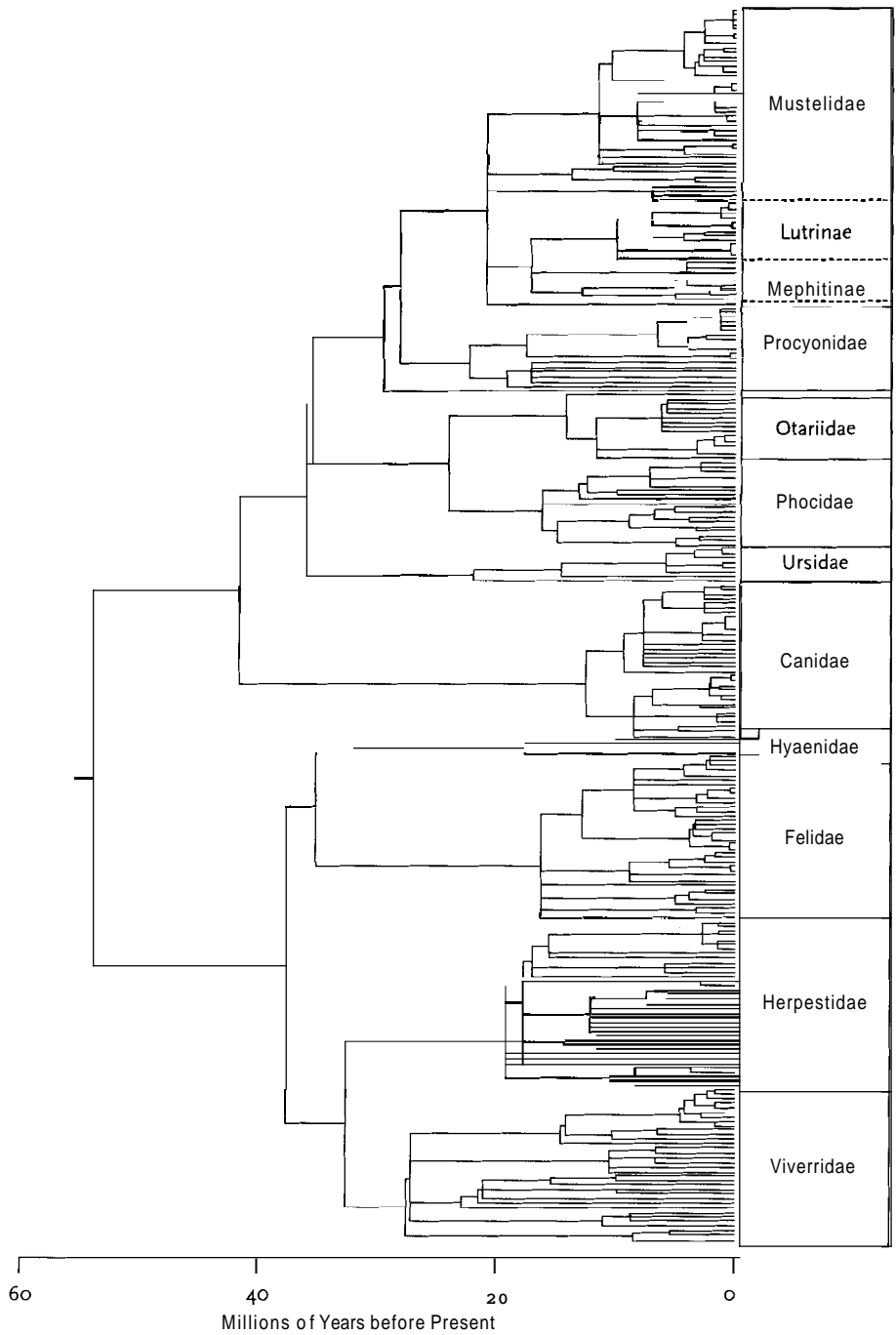


FIGURE 16.1. Complete supertree of the Carnivora. From Bininda-Emonds et al. (1999), with permission

TABLE 16.1
Multiple Regression Model across Primates and
Carnivores Predicting Extinction Risk in Declining Species

PREDICTOR	COEFFICIENT	<i>t</i>
Geographic range	-0.291	-7.65***
Trophic level	0.402	4.00***
Population density	-0.113	-2.06*
Gestation length	1.590	2.77**
Body mass	4.002	-0.02
Order ¹	-0.084	-1.53
Body mass x order ¹	0.704	3.33***
Gestation length x order ¹	-2.790	-2.80**

SOURCE: Data from Purvis et al. (2000)

NOTES: Sample size is 120 species, 112 contrasts. The model accounts for 47.6% of the total variance. All tests are two-tailed: *, $p = 0.05$; **, $p = 0.01$; ***, $p = 0.001$.

¹Carnivore = 0, primate = 1

gestation lengths are indicative of species with slow reproductive rates and, in turn, increased extinction risk, then it would also be useful to know whether the traits of these species are evolving at slower rates. In this way, supertrees help us to unify current factors related to extinction with longer evolutionary patterns, both of which are important for understanding how and why species become threatened (Cracraft, ; Eldredge 1999; Purvis et al. 2001).

CORRELATES OF EXTINCTION RISK

Some species have biological traits that increase their risk of extinction. There are many reviews of these characteristics and their underlying causal explanations (Lawton 1995; McKinney 1997; Simberloff 1998; Owens and Bennett 2000). Surprisingly, until recently, no statistical analysis revealed precisely which traits are actually more important than others, nor how these traits are differentially involved among taxa. Aside from lacking sufficiently large databases to carry out such studies, the rate-limiting step in most cases was the lack of a complete phylogeny. Consequently, supertrees have greatly aided in direct

tests of the biological correlates of extinction risk in bats, carnivores, and primates (Purvis et al. 2000, 2001; Jones et al. 2003), with other taxa currently being assessed. The following is a brief summary of this work and its relevance to giant pandas and carnivores.

Purvis et al. (2000) used the IUCN Red List as a proxy for extinction risk (see Hilton-Taylor 2000). Essentially, each of the threat levels given in the Red List was coded as a continuous character ranging from "lower risk" and "least concerned" to "extinct in the wild." A database was collated from the published literature on eight biological traits for each primate and carnivore species. Using the independent contrasts statistical analysis for each order (Purvis and Rambaut, 1995) multiple regression models were developed to find the best predictive variables for extinction risk. Among the many hypothesized traits, across carnivores and primates, four in particular explained up to 50% of the total between-species variation: high trophic level, low population density, slow life history, and especially a small geographic range size (table 16.1) There are also significant differences between the orders. Larger body mass is associated with extinction risk in

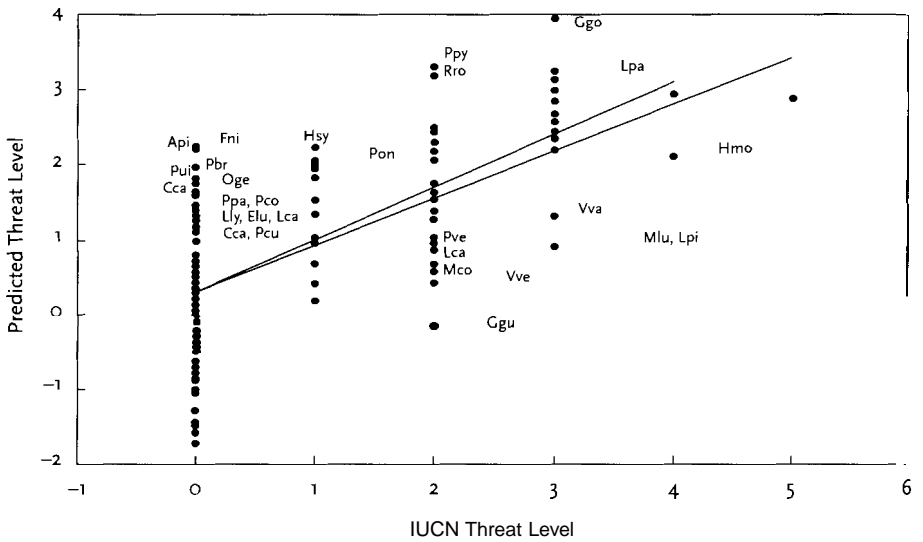


FIGURE 16.2. Predictions from multiple regression models for carnivores (upper line) and primates (lower line), plotted against IUCN threat categories. IUCN threat codes are scored as: 0, Lower Risk, Least Concern; 1, Lower Risk, Near Threatened; 2, Lower Risk, Conservation Dependent and Vulnerable; 3, Endangered; 4, Critically Endangered; 5, Extinct in the Wild and Extinct. Lines are least-squares regressions for each order. Species with residuals greater than 1.0 are coded on the graph as follows: Primates: *Alouatta pigra* (Api), *Cebus capucinus* (Cca), *Gorilla gorilla* (Ggo), *Hylobates moloch* (Hmo), *Hylobates syndactylus* (Hsy), *Lemur catta* (Lca), *Mirza coquereli* (Mco), *Papio ursinus* (Pui), *Pongo pygmaeus* (Ppy), *Propithecus verreauxi* (Pve), *Rhinopithecus roxellana* (Rro), *Varecia variegata* (Vva). Carnivores: *Caracal caracal* (Cca), *Enhydra lutris* (Elu), *Felis nigripes* (Fni), *Gulo gulo* (Ggu), *Lycaon pictus* (Lpi), *Lynx canadensis* (Lca), *Lynx lynx* (Lly), *Lynx pardinus* (Lpa), *Mustela lutreola* (Mlu), *Oncifelis geoffroyi* (Oge), *Panthera onca* (Pon), *Parahyaena brunnea* (Pbr), *Panthera pardus* (Ppa), *Pseudalopex culpaeus* (Pcu), *Puma concolor* (Pco), *Vulpes velox* (Vvu). Species classified by IUCN as Least Concern, with negative residuals, are not annotated, because there is no subdivision in the IUCN system among nonthreatened species, and these residuals therefore have little meaning.

primates, whereas gestation length is more important in carnivores. Taken together, these results show that some factors are more critically involved with processes of extinction than others. Specifically, characteristics that are indicative of population decline and small geographic ranges (rarity) are most salient, as indicated in other studies (Manne et al. 1999). However, some characteristics may only be important for particular taxa, such that biological correlates of extinction risk are, to a degree, taxon specific.

Given that multiple biological characteristics are related to the IUCN Red List, to what degree can our model predict which species are risk-prone? Figure 16.2 shows the predicted model plotted against the IUCN Red List. Overall, the fit

is remarkably good. The interesting patterns are revealed when we isolate species that fit above or below the regression line. For example, many of the felids, along with the giant panda, are predicted to have a higher extinction risk than currently listed. It is precisely these species that we would suggest should have greater protection and perhaps continual reassessment of their level of threat based on biological correlates. A good example is the sea otter (*Enhydra lutris*; denoted as Elu in figure 16.2), which was reduced in level of threat, but due to recent population declines is again being upgraded to threatened status (Estes et al. 1998). Conversely, there are several species that are classified as more threatened than their biology would suggest; these

TABLE 16.2

Characteristics of Giant Pandas Relative to Observed Correlates of Extinction in Bats, Primates, Carnivores, and Birds

TAXON	LARGE SIZE	SMALL RANGE	SLOW LIFE HISTORY	HIGH TROPIC LEVEL	LOW DENSITY
Giant pandas	Yes	Yes	Yes	No	Yes
Bats	No	Yes	Yes	—	—
Primates	Yes	Yes	No	Yes	Yes
Carnivores	No	Yes	Yes	Yes	Yes
Birds	Yes	—	Yes	—	—

SOURCES: Data for bats from Jones et al. (2002), primates and carnivores from Purvis et al. (2000) and birds from Owens and Bennett (2000).

NOTE: —, Not included in the analysis

include the wolverine (*Gulo gulo*) and wild dog (*Lycaon pictus*), which are currently experiencing massive habitat losses.

In sum, a phylogenetic analysis combined with a database of biological traits associated with extinction risk can be used in a predictive manner for explaining why some species are at risk and some are not. Across the taxa that have been analyzed phylogenetically for correlates of extinction risk (bats, primates, carnivores, birds), large body size, small geographic range distribution, slow life history, high trophic level, and low population density are significant (table 6.2). The giant panda shares all but one of these traits (trophic level). Thus, it is unsurprising that the giant panda is highly endangered. From this comparative analysis, we can now turn to the next important question involving how these traits differ in closely related taxa (ancestral carnivores) and whether they appear to have evolved in a different manner.

TRAITS OF EXTINCTION IN GIANT PANDAS

The giant panda is unique because of its bamboo diet and yet carnivore ancestry, its relatively large radial sesamoid (the so-called "panda's thumb"), and, of course, the adorable black-and-

white coloration. These pronounced traits are not typically associated with endangered status, although the conspicuous coloration undoubtedly increases the chances of poaching. The question is what characteristics are unusual for the giant panda that seem to relate to extinction risk and, in particular, are distinctive in comparison with other carnivores. As this volume conveys, a definitive answer cannot be given because we simply do not have all relevant information on behavior, ecology, life histories, and digestive physiology of the giant panda and other carnivores. There are, however, some clear patterns if we simply compare certain functional traits, such as life histories. It is well known that giant pandas have a relatively slow reproductive rate (Hu and Wei 1990; Schaller et al. 1995; Zhu et al. 2001). Reproductive rate in mammals is a composite of many traits, including gestation length, growth rate, age that eyes first open, weaning age, age at sexual maturity, interbirth interval, and longevity. Which traits seem to be different in giant pandas compared with other carnivores? The answer again involves using phylogenies to make comparisons.

An earlier study analyzed ten life history traits across the carnivores to test which ones were significantly different in the giant panda (Gittleman 1994). Surprisingly, most life histories in

the giant panda are very similar to those of other bears and carnivores. For example, the age at sexual maturity, weaning age, and even birth weight are not significantly different from expected patterns, once body size (allometry) is taken into account. Stark differences appear with early life histories, such as a slow growth rate (individual and total growth of litter) and a slightly long gestation length. In comparing other species that also have these markedly different life histories, there does not seem to be any consistent association with ecology, mating system, or phylogenetic heritage. The primary explanation seems to rest with age-specific mortality rates: taxa with slow life histories (e.g., most bears, many large cats) have relatively low mortality rates. Comparative trends across many mammal groups thus now show that life history variation is closely related to mortality schedules (Purvis and Harvey 1995). For example, across primates (Ross and Jones, 1999) and carnivores (Gittleman, 1993, 1994) species with high mortality rates reproduce at an early age and have high birth rates. The problem in the giant panda is that it deviates from this mammalian pattern: from the data available, mortality is relatively high, which would predict that life histories should be comparatively fast. These comparisons indicate that critical factors involved in mortality, either intrinsic (nutritional or reproductive physiology) and/or extrinsic (stress due to habitat loss), are more intense than would be predicted from life history evolution across mammals in general and carnivores in particular.

BIOLOGICAL TRAITS AND EVOLUTIONARY RATES

Large-scale taxonomic differences often result from changes in evolutionary rates. Evolutionary rates may occur fairly quickly, as in hourly generational changes in laboratory strains of fruit flies (*Drosophila*) to lineages of vertebrate fossils that change over millions of years (Gingerich 1993; Carroll 1997). With complete phylogenies, it is possible to not only measure more accurately the tempo and mode of how lineages

change but also how specific traits change among individual taxa (Gittleman et al. 1996). For example, evolutionary rates could be accelerated by reducing gestation length, age at sexual maturity, or interbirth interval. In the present context, it is important to ask whether evolutionary rates in the bear clade, including the giant panda, are different from other carnivore clades and which traits are evolving most rapidly. We can answer these questions by comparing sister taxa (see Martins 1994; Purvis et al. in press), or Webster et al. [2003] for further discussion about measuring evolutionary rates). Assuming that characters change by an assumed (Brownian) model of evolution, we can calculate the difference between the amount of change in a trait on one branch and that on another branch. The model of evolution is important: Brownian motion assumes there is no directionality to trait variation over time, thus resulting in the expectation that traits, although showing variation in the short term, are expected to have a net variation of zero in the long term. Sister-taxon comparisons are used because a pair of branches descends from each node to give an independent estimate of rate, so rates can be compared between groups.

Using supertrees, Purvis et al. (in press) showed that carnivores evolve at slow rates: body mass, age at maturity, gestation length, and interbirth interval all evolve at significantly reduced rates in carnivores compared with primates. The one exception is litter size, which is most likely due to most primates having a litter size of one and therefore showing little variance in this trait. What is important about the giant panda, along with related ursids, is that when this clade is compared with other carnivores, gestation length and interbirth interval evolve significantly faster (table 16.3) than Lutrinae/Mephitinae, Canidae, Felidae, and Viverridae. Significantly, this deviation does not seem to involve large body mass: significant differences in evolutionary rates among life histories does not consistently correlate with size per se. Combined with the above comparative results indicating that the giant panda has a number of

CLADE	ASM	BM	GL	IBI	LS
Mustelinae	1.39	24.17	0.81	1.20	29.05
Lutrinae-Mephitinae	1.96	7.29	0.25	0.20	17.56
Phocidae-Otariidae	—	6.09	—	1.08	—
Canidae	0.94	8.27	0.06	0.27	50.15
Felidae	2.12	23.58	0.20	2.83	42.34
Hepestidae	0.87	9.41	0.47	2.20	22.41
Viverridae	1.09	2.93	0.18	0.47	17.97
Ursidae	1.29	14.38	1.04	4.32	12.44
Significance level	ns	ns		t	ns

NOTES: ASM, age at sexual maturity; BM, body mass; CL, gestation length; IBI, interbirth interval; LS, litter size, ns, not significant; *, $p = 0.05$; —, no data.

extinction-prone traits, the panda is characterized by extreme variability in evolutionary rates for some fundamental reproductive characteristics (gestation length, interbirth interval). These phylogenetic patterns may indicate that, as in other taxa (McKinney and Gittleman 1995), the giant panda is showing features that indicate responses to environmental stress.

CONCLUSIONS

It is depressingly true that not all species will survive. Giant pandas, due to their charismatic nature, endearing biological qualities, and our willingness to protect them, may not go extinct in our lifetimes. Nevertheless, we can certainly learn from the panda's proclivity to extinction risk and from many other species that are similarly risk-prone. A broad-scale phylogenetic approach permits us to find those particular biological traits that consistently correlate with risk across independent lineages. In essence, phylogenies can provide a short cut to which species are likely to be endangered and perhaps go extinct in the near future. Conservation biology needs as many tools as possible. Using phylogenies to examine the comparative biology of

threatened species like the giant panda will not only help this magnificent species but also leave a legacy to protect many other similar species.

ACKNOWLEDGMENTS

We thank Devra Kleiman for organizing the symposium at which the original paper was delivered, and Don Lindburg for an invitation to the Panda 2000 conference and for his patience in considering this chapter. We also thank Kate Jones for suggesting this collaboration.

REFERENCES

- Barraclough, T. G., A. P. Vogler, and P. H. Harvey. 1999. Revealing the factors that promote speciation. In *Evolution of biodiversity*, edited by A. E. Magurran and R. M. May, pp. 202–19. Oxford: Oxford University Press.
- Baum, B. R. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon* 41:3–10.
- Bininda-Emonds, O. R. P. 2000. Factors influencing phylogenetic inference: A case study using the mammalian carnivores. *Mol Phylogenet Evol* 16: 113–26.
- Bininda-Emonds, O. R. P., and M. J. Sanderson. 2001. Assessment of the accuracy of matrix representation

- with parsimony supertree construction. *Syst Biol* 50:575-79.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and A. A. Purvis. 1999. Building large trees by combining phylogenetic information: A complete phylogeny of the extant Carnivora (Mammalia). *Biol Rev* 74: 143-75.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and M. A. Steel. 2002. The (super)tree of life: Procedures, problems, and prospects. *Annu Rev Ecol Syst* 33: 265-89.
- Carroll, R. L. 1997. *Patterns and processes of vertebrate evolution*. New York: Cambridge University Press.
- Cracraft, J. 1992. Explaining patterns of biological diversity: Integrating causation at different spatial and temporal scales. In *Systematics, ecology, and the biodiversity crisis*, edited by N. Eldredge, pp. 59-76. New York: Columbia University Press.
- Diamond, J. 1989. Overview of recent extinctions. In *Conservation for the twenty-first century*, edited by D. Western and M. Pearl, pp. 37-41. New York: Oxford University Press.
- Eldredge, N. 1999. Cretaceous meteor showers, the human ecological "niche," and the sixth extinction. In *Extinctions in near time*, edited by R. D. E. Macphee, pp. 1-14. New York: Kluwer.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and near-shore ecosystems. *Science* 282:473-76.
- Gingerich, P. D. 1993. Quantification and comparison of evolutionary rates. *Am / Sci* 293A: 453-78.
- Gittleman, J. L. 1993. Carnivore life histories: A re-analysis in the light of new models. In *Mammals as predators*, edited by N. Dunstone and M. L. Gorman, pp. 65-86. Oxford: Oxford University Press.
- Gittleman, J. L. 1994. Are the pandas successful specialists or evolutionary failures? *BioScience* 44: 456-64.
- Gittleman, J. L. 2001. Hanging bears from phylogenetic trees: Investigating patterns of macroevolution. *Ursus* 11:29-40.
- Gittleman, J. L., C. G. Anderson, M. Kot, and H.-K. Luh. 1996. Comparative test of evolutionary liability and rates using molecular phylogenies. In *New uses for new phylogenies*, edited by P. H. Harvey, A. J. L. Brown, J. Maynard Smith, and S. Nee, pp. 289-307. Oxford: Oxford University Press.
- Harvey, P. H., A. J. L. Brown, J. Maynard Smith, and S. Nee. 1996. *New uses for new phylogenies*. Oxford: Oxford University Press.
- Hillis, D. M. 1997. Biology recapitulates phylogeny. *Science* 276:218-19.
- Hilton-Taylor, C., ed. 2000. 2000 *IUCN red list of threatened species*. Gland, Switzerland, and Cambridge: IUCN—The World Conservation Union.
- Hu, J., and F. Wei. 1990. Development and progress of breeding and rearing giant pandas in captivity within China. In *Research and progress in biology of giant pandas*, edited by H. Jinchu, pp. 32-25. Sichuan: Sichuan Publishing House of Science and Technology.
- Jones, K. E., A. Purvis, A. Maclarnon, O. R. P. Bininda-Emonds, and N. Simmons. 2002. A phylogenetic supertree of the extant bats (Mammalia: Chiroptera). *Biol Rev* 77:223-59.
- Jones, K. E., J. L. Gittleman, and A. Purvis. 2003. Biological correlates of extinction risk in bats. *Am Nat* 161:601-14.
- Lawton, J. H. 1995. Population dynamic principles. In *Extinction rates*, edited by J. H. Lawton and R. M. May, pp. 147-63. Oxford: Oxford University Press.
- Liu, F.-G. R., M. M. Miyamoto, N. P. Freire, P. W. Ong, M. R. Tennant, T. S. Young, and K. F. Gugel. 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Science* 291: 1786-89.
- Manne, L. L., T. M. Brooks, and S. L. Pimm. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399:258-61.
- Martins, E. 1994. Estimating the rate of phenotypic evolution from comparative data. *Am Nat* 144:193-209.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological perspectives. *Annu Rev Ecol Syst* 28:495-516.
- McKinney, M. L., and J. L. Gittleman. 1995. Ontogeny and phylogeny: Tinkering with covariation in life history, morphology and behaviour. In *Evolutionary change and heterochrony*, edited by K. J. McNamara, pp. 21-46. New York: John Wiley and Sons.
- O'Brien, S. J., E. Eizirik, and W. J. Murphy. 2001. On choosing mammalian genomes for sequencing. *Science* 292:2264-65.
- Owens, I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proc Nat Acad Sci USA* 97:12144-48.
- Purvis, A. A. 1995. Composite estimate of primate phylogeny. *Phil Trans Roy Soc Lond B* 348:405-21.
- Purvis, A. A. 1996. Using interspecies phylogenies to test macroevolutionary hypotheses. In *New uses for new phylogenies*, edited by P. H. Harvey, A. J. L. Brown, J. Maynard Smith, and S. Nee, pp. 153-68. Oxford: Oxford University Press.
- Purvis, A. A., and P. H. Harvey. 1995. Mammal life history: A comparative test of Charnov's model. *J Zool (Lond)* 237:259-83.

- Purvis, A. A., and A. Hector. 2000. Getting the measure of biodiversity. *Nature* 405:212–19.
- Purvis, A. A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Computer Applications Biosci* 11:247–51.
- Purvis, A. A., and A. J. Webster. 1999. Phylogenetically independent comparisons and primate phylogeny. In *Comparative primate socioecology*, edited by P. C. Lee, pp. 44–70. Cambridge: Cambridge University Press.
- Purvis, A. A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proc R Soc Lond B* 267:1947–52.
- Purvis, A. A., G. M. Mace, and J. L. Gittleman. 2001. Past and future carnivore extinctions: A phylogenetic perspective. In *Carnivore conservation*, edited by J. L. Gittleman, S. Funk, D. Macdonald, and R. K. Wayne, pp. 11–34. Cambridge: Cambridge University Press.
- Purvis, A. A., A. J. Webster, P.-M. Agapow, K. E. Jones, and N. J. B. Isaac. In press. Primate life histories and phylogeny. In *Primate life histories and socioecology*, edited by P. M. Kappeler and M. Pereira. Chicago: University of Chicago Press.
- Ragan, M. A. 1992. Phylogenetic inference based on matrix representation of trees. *Mol Phylogenet Evol* 1:53–58.
- Ross, C., and K. E. Jones. 1999. Socioecology and the evolution of primate reproductive rates. In *Comparative primate socioecology*, edited by P. C. Lee, pp. 73–110. Cambridge: Cambridge University Press.
- Sanderson, M. J., A. A. Purvis, and C. Henze. 1998. Phylogenetic supertrees: Assembling the trees of life. *Trends Ecol Evol* 13:105–9.
- Schaller, G. B., J. Hu, W. Pan, and J. Zhu. 1985. *The giant pandas of Wolong*. Chicago: University of Chicago Press.
- Sechrest, W., T. M. Brooks, G. A. B. da Fonseca, W. R. Konstant, R. A. Mittermeier, A. A. Purvis, A. B. Rylands, and J. L. Gittleman. 2002. Hotspots and the conservation of evolutionary history. *Proc Nat Acad Sci USA* 99:2067–71.
- Simberloff, D. 1998. Small and declining populations. In *Conservation science and action*, edited by W. J. Sutherland, pp. 116–34. Oxford: Blackwell Science.
- Springer, M. S., and W. W. de Jong. 2001. Which mammalian supertree to bark up? *Science* 291:1709–11.
- Vázquez, D. P., and J. L. Gittleman. 1998. Biodiversity conservation: Does phylogeny matter? *Curr Biol* 8:R379–81.
- Webster, A. J., J. L. Gittleman, and A. A. Purvis. 2003. The life history legacy of evolutionary body size change in carnivores. *J Evol Biol* 17:1–12.
- Zhu, X., D. G. Lindburg, W. Pan, K. A. Forney, and D. Wang. 2001. The reproductive strategy of giant pandas (*Ailuropoda melanoleuca*): Infant growth and development and mother-infant relationships. *J Zool (Lond)* 253:141–55.