

Evidence for the Role of Infectious Disease in Species Extinction and Endangerment

KATHERINE F. SMITH,* ‡ DOV F. SAX,* AND KEVIN D. LAFFERTY†

*University of Georgia, Institute of Ecology, Athens, GA 30602, U.S.A.

†USGS Channel Islands Field Station, University of California Santa Barbara, Marine Science Institute, Santa Barbara, CA 93106, U.S.A.

Abstract: *Infectious disease is listed among the top five causes of global species extinctions. However, the majority of available data supporting this contention is largely anecdotal. We used the IUCN Red List of Threatened and Endangered Species and literature indexed in the ISI Web of Science to assess the role of infectious disease in global species loss. Infectious disease was listed as a contributing factor in <4% of species extinctions known to have occurred since 1500 (833 plants and animals) and as contributing to a species' status as critically endangered in <8% of cases (2852 critically endangered plants and animals). Although infectious diseases appear to play a minor role in global species loss, our findings underscore two important limitations in the available evidence: uncertainty surrounding the threats to species survival and a temporal bias in the data. Several initiatives could help overcome these obstacles, including rigorous scientific tests to determine which infectious diseases present a significant threat at the species level, recognition of the limitations associated with the lack of baseline data for the role of infectious disease in species extinctions, combining data with theory to discern the circumstances under which infectious disease is most likely to serve as an agent of extinction, and improving surveillance programs for the detection of infectious disease. An evidence-based understanding of the role of infectious disease in species extinction and endangerment will help prioritize conservation initiatives and protect global biodiversity.*

Keywords: IUCN, wildlife disease

Evidencia del Papel de Enfermedades Infecciosas en la Extinción y Puesta en Peligro de Especies

Resumen: *Las enfermedades infecciosas están consideradas entre las cinco causas principales de la extinción global de especies. Sin embargo, la mayoría de los datos disponibles que sustentan esta afirmación son anecdóticos. Utilizamos la Lista Roja de Especies Amenazadas y en Peligro de la IUCN y literatura indexada en la Red ISI de Ciencia para evaluar el papel de las enfermedades infecciosas en la pérdida global de especies. Las enfermedades infecciosas fueron identificadas como un factor contribuyente a <4% de las extinciones conocidas desde 1500 (833 especies de plantas y animales) y como un factor contribuyente al estatus de críticamente en peligro en <8% de los casos (2852 especies de plantas y animales en peligro crítico). Aunque parece que las enfermedades infecciosas juegan un papel menor en la pérdida global de especies, nuestros hallazgos subrayan dos limitaciones importantes en la evidencia disponible: incertidumbre acerca de las amenazas a la supervivencia de especies y un sesgo temporal en los datos. Varias iniciativas podrían ayudar a sobreponer esos obstáculos, incluyendo pruebas científicas rigurosas para determinar qué enfermedades infecciosas son una amenaza significativa al nivel de especie, reconocimiento de las limitaciones asociadas con la ausencia de datos básicos del papel de enfermedades infecciosas en la extinción de especies, combinación de datos con teoría para discernir las circunstancias bajo las cuales es más probable que una enfermedad infecciosa funcione como agente de extinción y mejoramiento de los programas de vigilancia para la detección de enfermedades infecciosas. El entendimiento, basado en evidencia, del papel de las enfermedades infecciosas en la extinción*

‡email smithk@uga.edu

Paper submitted August 23, 2005; revised manuscript accepted March 14, 2006.

y puesta en peligro de especies ayudará a priorizar iniciativas de conservación y proteger la biodiversidad global.

Palabras Clave: enfermedades de vida silvestre, IUCN

Introduction

Recent studies suggest that infectious diseases in wildlife populations are emerging at unusually high rates (Harvell et al. 1999, 2002; Epstein 2001). Emerging infectious diseases (EIDs) are those caused by parasites and pathogens that have recently increased in incidence, occupied host species or geographic extent; have been newly discovered; or are caused by a newly evolved agent (Lederberg et al. 1992; Daszak et al. 2000). The diversity of EIDs afflicting wildlife, coupled with the fear that an increased frequency of outbreaks will occur in the future, have raised concern that infectious disease may play a strong role in species extinction (Holmes 1996; Daszak et al. 2000; Harvell et al. 2002). Indeed, infectious diseases can extirpate local populations, mediate community dynamics, and shrink host ranges (McCallum & Dobson 1995; Daszak et al. 1999; Lafferty 2003; Walsh et al. 2003).

Given the effects of infectious diseases on wildlife, it is not surprising that a survey of biologists listed infectious disease among the top five causes of species extinctions in the United States (Wilcove et al. 1998). However, the majority of available data supporting this contention is largely anecdotal. Moreover, epidemiological theory predicts that infectious diseases should only drive species to extinction under specific circumstances—most commonly when pre-epidemic population size is small, reservoir hosts are available, or when the infectious agent can survive in the abiotic environment (de Castro & Bolker 2005). In response to a growing interest in global species loss and emerging infectious diseases, it is worth investigating the generalization that infectious diseases play a widespread role in species extinction.

We used the World Conservation Union (IUCN) Red List of Threatened and Endangered Species (IUCN 2004) and the Science Citation Index Expanded (ISI Web of Science) to compile the most comprehensive information available on the causal role of infectious disease in species extinction. In doing so, we sought to accomplish three goals. First, to discern what the available evidence suggests about the causal role of infectious disease in species extinction and critical endangerment. Second, to uncover limitations of the data that may influence these results. Third, to use this knowledge to suggest priority areas for future research on wildlife infectious diseases.

IUCN Database and Literature Search

Designed for global taxon assessments, the IUCN Red List is the most exhaustive database available of species of

conservation concern and those documented to have become extinct in the past 500 years. It has been used repeatedly to assess the impact of individual and multiple threats in the global loss of biodiversity and for specific groups (e.g., Butchart et al. 2004; Gurevitch & Padilla 2004; Clavero & Garcia-Berthou 2005). The IUCN Red List reports more than 38,000 plants and animals whose status is categorized based on a defined set of criteria as extinct, extinct in the wild, critically endangered, endangered, vulnerable, lower risk, near threatened, data deficient, or of least concern (IUCN 2004). The database is a searchable classification of major species threats (e.g., habitat loss, overexploitation, invasive species) ordered in a hierarchical manner and reported as “summary documentation” for each species case. “Pathogens and parasites” (referred to hereafter as infectious diseases) are classified as threat types under “invasive alien species” (threat 2.4) and “changes in native species dynamics” (threat 8.5) (IUCN 2004). Because this classification system has only been applied to a fraction of species in the database (Clavero & Garcia-Berthou 2004), we individually examined the “detailed documentation” of all records of extinct and critically endangered plants and animals in the IUCN Red List (IUCN 2004) to determine those threatened by infectious disease. We included the 60 species listed as extinct in the wild (those that exist only in captivity) in our tally of extinct species. Given the breadth of the IUCN Red List, we focused on these threat categories because they are most informative to our goals and arguably of greatest conservation concern.

The IUCN Red List reports only threats that trigger listing of the taxon concerned and does not rank or fully elucidate the relative importance of individual threats (IUCN 2004). Threats are reported as having occurred in the past and/or present and/or future, based on a time frame of three generations or 10 years, whichever is longer (not exceeding 100 years in the future) (IUCN 2004). A threat that occurred in the past, is occurring in the present, or may occur in the future is cited as ongoing (IUCN 2004). For each species account, we recorded the time frame of the threat. Based on the information reported in the detailed documentation, we tallied a fourth category: hypothesized threat. For example, the summary documentation often reported infectious disease as a contemporary or ongoing threat, whereas the detailed documentation made it clear that the threat was only a hypothesis, that no evidence existed to support the claim, or that ongoing research was attempting to discern the threat of infectious disease (e.g., descriptions for the critically endangered toad *Atelopus andinus* and frog *Taudactylus*

acutirostris). For accounts such as this, the threat of infectious disease was recorded as hypothesized.

We also conducted a literature survey using the ISI Web of Science to uncover extinct and critically endangered species threatened by infectious disease that may have been missed by the IUCN specialist groups or that have not been incorporated into the IUCN Red List yet. We searched for papers published between 1945 and 2004 with titles, key words, or abstracts with the following general search strings:

For extinct animals: ((extinct*) and (animal* or faun*) and (disease* or pathogen* or parasit* or bacteri* or fung* or protozoa*) not (human)). Total returns: 143.

For extinct plants: ((extinct*) and (plant* or flor*) and (disease* or pathogen* or parasit* or bacteri* or fung* or protozoa*) not (human)). Total returns: 195.

For critically endangered animals: ((threat* or endanger*) or (mass and mortalit*) and (animal* or faun*) and (disease* or pathogen* or parasit* or bacteri* or fung* or protozoa*) not (human)). Total returns: 798

For critically endangered plants: ((threat* or endanger* or (mass and mortalit*) and (plant* or flor*) and (disease* or pathogen* or parasit* or bacteri* or fung* or protozoa*) not (human)). Total returns: 687.

Abstracts or full manuscripts were obtained for articles containing information describing the extinction or critical endangerment of a species threatened by infectious disease. Following the IUCN (2004) criteria for assessing threat status (extinct, critically endangered, etc.), the South Pacific land snail *Partula turgida* was the sole species we identified that should have been included on the IUCN Red List of extinctions facilitated by infectious disease but was not (Table 1). Our literature survey did not uncover any critically endangered animals or plants threatened by infectious disease that were not already on the IUCN Red List. Although the ISI Web of Science does not include gray literature, we believe our reference base was representative of species extinctions and contemporary threats relevant to this study.

Infectious Disease as a Factor in Species Extinction and Endangerment

Infectious disease was infrequently listed as a contributing factor to species extinction or endangerment. The IUCN Red List (IUCN 2004) reports that in the past 500 years, 100 plant and 733 animal species are known to have gone extinct. Whereas multiple causal factors are typically listed as having contributed to a species' extinction, the most common causes appear to be habitat loss and overexploitation (IUCN 2004). Of these 833 known species extinctions, only 31 cases (3.7%) have been attributed, at least in part, to infectious disease (Table 1).

Whereas some forces, such as habitat loss or overexploitation, are listed as the single causal driver of a species' extinction, in no case is infectious disease listed alone

(IUCN 2004). This raises the possibility that infectious disease is less likely than other drivers of species extinction to act in isolation. To assess this possibility, we tested the null hypothesis that the distribution of the observed number of species for which infectious disease is the sole or contributing (one of multiple) threat is the same as that expected by random chance alone. We tallied the total number of threats reported for each extinct and critically endangered species and noted which of these included the threat of infectious disease. The expected (E) number of species for which infectious disease was the sole or contributing threat was calculated using the following formula and was used to generate the expected distributions in Fig. 1:

$$E = \frac{D \cdot X}{N},$$

where D is the number of species for which infectious disease is a listed threat, X is the number of species that experience a given number of threats (determined for 1–30 threats; 30 was the maximum number of threats reported for a single species), and N is the number of species (excluding those for which no threats are listed or are reported as “unknown”).

A Kolmogorov–Smirnov goodness-of-fit test rejected the null hypothesis that the observed distribution of extinct species is the same as the expected distribution ($D_{\max} = 0.461$, $n = 31$, $p = 0.003$). The most apparent difference in these distributions is the complete lack of observed instances in which the disease acted alone to cause species extinctions. This finding conforms to theoretical models that suggest infectious disease alone is unlikely to cause species extinctions, particularly for infectious diseases with density-dependent transmission that are host specialists (Anderson & May 1992). Infectious diseases with frequency-dependent or spatial transmission, those that use reservoir hosts or afflict small populations may be more likely to be the sole cause of species extinction (de Castro & Bolker 2005).

Although the IUCN Red List cites species extinctions as far back as 1500, infectious disease is only reported as a causal mechanism for those occurring after the mid 1800s (Table 1), when definitive tests for determining the causality of infectious diseases were put into practice. Given this lack of baseline data we could not confidently assess the role of infectious disease in species extinctions prior to 1900. We were able to consider the importance of infectious disease in species extinctions occurring in the twentieth century, when records of species loss and the ability to detect infectious disease were greatly improved. After excluding species extinctions prior to 1900, the 25 subsequent extinctions purportedly linked to infectious disease represent <4% of the known plant and animal species extinctions (631 animal and 93 plant extinctions) (Fig. 2).

The IUCN Red List (IUCN 2004) reports 1490 plant and 1362 animal species as critically endangered. Of these

Table 1. Known species extinctions purportedly facilitated by disease since 1500.

Class	Species	Distribution	Date ^a	Causal factors
Aves	<i>Akialoa ellisiana</i>	Hawaiian Islands	1837c	habitat loss; disease from introduced species ^b
	<i>Akialoa stejnegeri</i>	Hawaiian Islands	1969r	habitat loss; disease from introduced species
	<i>Akialoa lanaiensis</i>	Hawaiian Islands	1892c	habitat loss; disease from introduced species
	<i>Akialoa obscura</i>	Hawaiian Islands	1940r	habitat loss; disease from introduced species; hunting
	<i>Corvus hawaiiensis</i> ^c	Hawaiian Islands	2002r	habitat loss; disease from introduced species; hunting
	<i>Drepanis pacifica</i>	Hawaiian Islands	1899r	habitat loss; disease from introduced species; hunting
	<i>Hemignathus obscurus</i>	Hawaiian Islands	1940r	habitat loss; disease from introduced species
	<i>Mobo apicalis</i>	Hawaiian Islands	1837c	habitat loss; disease from introduced species
	<i>Mobo bishopi</i>	Hawaiian Islands	1915e	habitat loss; disease from introduced species
	<i>Mobo braccatus</i>	Hawaiian Islands	1985r	habitat loss; predation and disease from introduced species; natural disaster
	<i>Mobo nobilis</i>	Hawaiian Islands	1934r	habitat loss; disease from introduced species
	<i>Myadestes myadestinus</i>	Hawaiian Islands	1989r	habitat loss; competition and disease from introduced species; natural disaster
	<i>Paroreomyza flammea</i>	Hawaiian Islands	1963r	habitat loss; disease from introduced species
	<i>Fregilupus varius</i>	Mascarene Islands	1860e	habitat loss; disease from introduced species; natural disaster
	<i>Heteralocha acutirostris</i>	New Zealand	1907r	habitat loss; disease from introduced species; hunting
	<i>Coturnix novaezelandiae</i>	New Zealand	1875e	habitat loss; predation and disease from introduced species
	<i>Ectopistes migratorius</i>	North America	1900e	habitat loss; disease from introduced species; hunting; intrinsic factors
	<i>Psephobus pulcherrimus</i>	Australia	1927r	habitat loss; predation and disease from introduced species; hunting; natural disaster; changes in native species dynamics
	Mammalia	<i>Nesoryzomys darwini</i>	Galapagos Islands	1930c
<i>Nesoryzomys indefessus</i>		Galapagos Islands	1934c	predation; competition and disease from introduced species
<i>Thylacinus cynocephalus</i>		Australia	1930r	habitat loss; competition and disease from introduced species; hunting
Amphibia	<i>Atelopus ignescens</i>	Ecuador	1988r	predation from introduced species; pollution; natural disaster; disease due to changes in native species dynamics
	<i>Atelopus longirostris</i>	Ecuador	1989r	habitat loss; pollution; disease due to changes in native species dynamics
	<i>Bufo baxteri</i> ^c	U.S.A.	2002r	habitat loss; pollution; disease from introduced species; disease due to changes in native species dynamics
	<i>Bufo periglenes</i>	Costa Rica	1989r	pollution; disease due to changes in native species dynamics; intrinsic factors
	<i>Eleutherodactylus chrysozetetes</i>	Honduras	1989r	habitat loss; pollution; natural disaster; disease due to changes in native species dynamics; intrinsic factors; human disturbance
	<i>Eleutherodactylus milesi</i>	Honduras	1989r	habitat loss; pollution; natural disaster; disease due to changes in native species dynamics; intrinsic factors; human disturbance
	<i>Rheobatrachus silus</i>	Australia	1979r	habitat loss; harvesting; pollution; disease due to changes in native species dynamics; human disturbance
	<i>Rheobatrachus vitellinus</i>	Australia	1985r	habitat loss; harvesting; pollution; disease due to changes in native species dynamics
	<i>Taudactylus diurnus</i>	Australia	1979r	habitat loss; harvesting; pollution; disease due to changes in native species dynamics; intrinsic factors; human disturbance
Gastropoda	<i>Partula turgida</i> ^d	Raiatea	1996e	predation from introduced species; microsporidian parasite in culture

^aDate of extinction defined as last reported in the wild (r), last collected (c), extinct (e) (IUCN 2004).

^bReferred to as parasites and pathogens in the IUCN database.

^cDenotes species extinct in the wild.

^dCausal mechanisms listed for *P. turgida* are from Cunningham and Daszak (1998). The reader should consult the IUCN Red List directly for detailed information on the causal factors contributing to the species extinctions listed here.

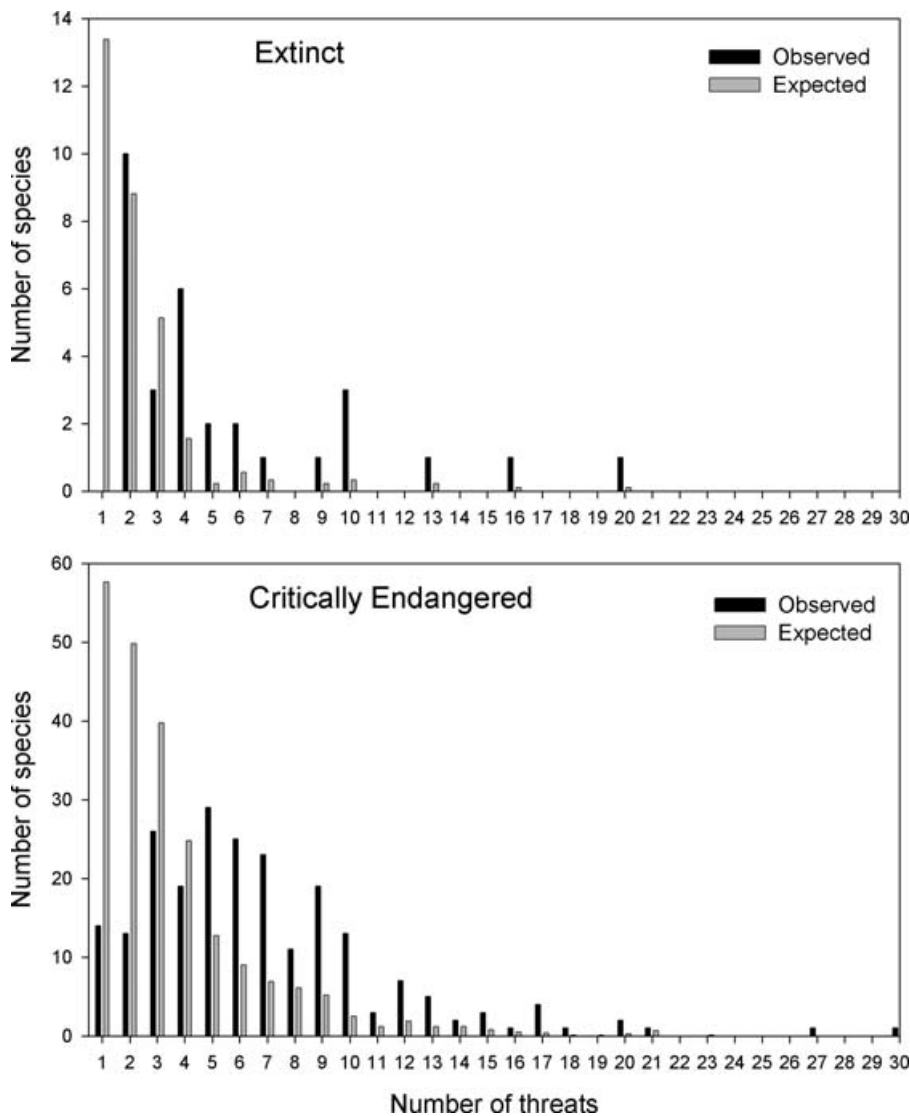


Figure 1. Distributions of the observed and expected number of extinct and critically endangered species for which infectious disease was the sole or contributing threat (one of multiple).

2852 critically endangered species, 223 have infectious disease listed as a contributing threat (IUCN 2004). This cohort of 223 species represents <8% of all critically endangered species. More than 75% of these are amphibians, although in many of these cases infectious disease is only a hypothesized or predicted threat (Fig. 2b). The majority of critically endangered species threatened by infectious disease have between three and seven additional contributing threats. Similar to the extinct species discussed above, few critically endangered species are threatened solely by infectious disease. This is in contrast to the expected null distribution, which predicts a far greater number of critically endangered species to be threatened by infectious disease alone ($D_{\max} = 0.454$, $n = 223$, $p < 0.001$) (Fig. 1).

Uncertainty in the Evidence

The IUCN Red List and similar data sets are invaluable resources for initiating broad-scale investigations into the

relative causes of global species loss. They are not, however, without limitations. Regardless, the information garnered from such data sets provides qualitative insight that is more cogent than that gained from anecdotal evidence or generalization. The results of our examination of the IUCN Red List and in-depth literature survey show that infectious disease does not appear to be a common agent of species extinction or critical endangerment. However, our results may be confounded by the nature of the evidence available. In particular, a level of uncertainty surrounding the actual threat of infectious disease and temporal bias in the data may contribute to our findings.

Uncertainty of Threat

Uncertainty surrounding the criteria used to categorize species' status for the IUCN Red List has received a wealth of attention (e.g., Akcakaya et al. 2000; Possingham et al. 2002; Lamoreux et al. 2003). In contrast, the uncertainty that surrounds the threats associated with each species'

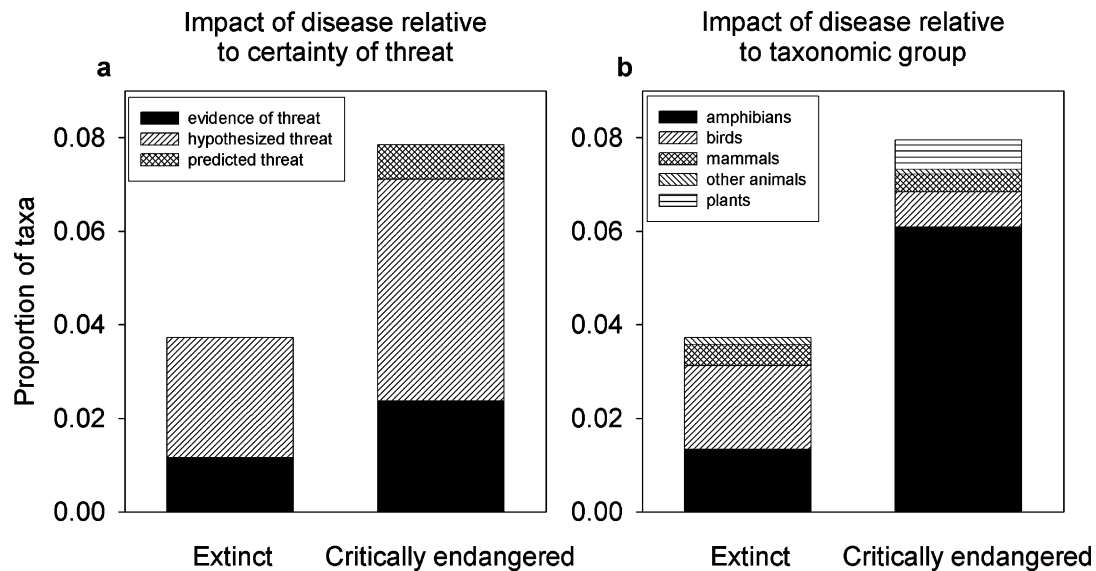


Figure 2. (a) Proportion of known species extinctions facilitated by disease (after 1900) and critically endangered species threatened by disease according to the World Conservation Union Red List (IUCN 2004). Evidence of threat is the proportion of taxa for which the threat is ongoing or present, hypothesized threat is the proportion of taxa for which the threat is only a hypothesis (no evidence currently exists to support the claim or ongoing research is attempting to discern the threat of disease), and predicted threat is the proportion of taxa for which disease is expected to be a threat in the future. (b) Proportion of known species extinctions facilitated by disease (post 1900) and critically endangered species threatened by disease depicted by taxonomic group. "Other animals" include invertebrates, fishes, and reptiles. (Extinct: amphibians, $n = 9$; birds, $n = 18$; mammals, $n = 3$; other animals, $n = 1$; plants $n = 0$. Critically endangered: amphibians, $n = 174$; birds, $n = 21$; mammals, $n = 11$; other animals, $n = 3$; plants $n = 18$.)

listing has warranted relatively little attention. The IUCN Red List makes no attempt to systematically rank these threats, making it difficult to discern the relative impact of infectious disease in the extinction or critical endangerment of a given species. In some cases additional research reveals that infectious disease is a major threat or cause of extinction. This appears to be the case for the numerous Hawaiian bird extinctions linked to avian pox and malaria (Table 1) (Van Riper & Scott 2001; Van Riper et al. 2002). In other cases, research suggests that infectious disease played a relatively minor, if not questionable, role in extinction. For example, the IUCN Red List cites hunting pressure, habitat loss, infectious disease, and intrinsic factors as contributing to the extinction of the Passenger Pigeon (*Ectopistes migratorius*) (Table 1). However, it is widely believed that heavy hunting pressure and the loss of habitat were the primary causes of extinction, whereas the contribution of infectious disease is questionable (e.g., Schorger 1955).

To better understand how infectious disease compares with other threats, we examined the 223 critically endangered species listed as threatened by infectious disease. In the majority of these cases, no conclusive evidence exists to support infectious disease as a contributing threat. More than half were only hypothesized to be threatened by infectious disease or predicted to be threatened in

the future (Fig. 2a). Indeed, the IUCN Red List includes threats posed by yet undiscovered or future events of low probability but with severe consequences (IUCN 2004). The argument for doing this is that certain threats, particularly those for which the effects are irreversible, must be identified early so as to facilitate appropriate conservation action (IUCN 2004). Although this may lead to inaccurate conclusions when tallies such as ours cannot discern the relative importance of listed threats, erring on the side of caution can be critical to species conservation. The global decline in amphibians provides a striking example of the potential discord between the IUCN Red List and real-world events.

Amphibians account for 30% of critically endangered animals and more than 75% of the critically endangered species threatened by infectious disease. The infectious fungus chytridiomycosis is listed as a contributing threat for more than 40% of these (IUCN 2004). Although chytridiomycosis has been reported in critically endangered amphibian species spanning six families, the IUCN (2004) lists the fungus only as a hypothesized or potential future threat for the majority (approximately 97%) of these. It is widely believed, however, that chytridiomycosis is the most significant threat to critically endangered amphibians (Berger et al. 1998; Daszak et al. 1999; Stuart et al. 2004), illustrating the discrepancy that can exist

between the IUCN Red List and real-time science. In the case of amphibians, it is critical that we do not underestimate the scope of chytridiomycosis because numerous factors make the fungus a significant conservation concern and a priority for biological research, including global distribution, rapid spread, a broad diversity of host species, and high virulence (Daszak et al. 1999). Moreover, the rapid population declines in populations infected with chytridiomycosis are characteristic of those observed when novel pathogens infect a population, a scenario that can facilitate extinction (Anderson & May 1986; de Castro & Bolker 2005).

Temporal Bias

There is concern that infectious diseases have been emerging recently at unusually high rates (e.g., Daszak et al. 1999; Harvell et al. 1999; Epstein 2001). Such an increase could explain why infectious disease is linked with a higher percentage of critically endangered species than extinct species. In addition, one might expect there to be a concordant increase in infectious disease-induced extinctions through time. However, such patterns could easily be confounded by an increase in our ability to detect infectious disease (see Ward & Lafferty 2004). Unfortunately, the lack of good baseline data on the role of infectious disease in extinctions prior to the late 1800s preclude a fair evaluation of this hypothesis. Furthermore, it is difficult to assess the historical role of infectious disease in species extinctions, given the lack of adequately preserved tissue. As a result, attempts to infer historical trends in the role of infectious disease as a threat to wildlife should be treated with caution.

Plants provide a striking example of the potential for temporal bias in the available evidence. Infectious diseases of plants are listed as causes of critical endangerment but not extinction. This could be due to an increase in the role of infectious disease as a threat to plants, evidence that infectious disease does not cause plant extinctions, or temporal bias in the data. Some infectious plant diseases that have caused massive population declines in abundant species (e.g., chestnut blight, dutch-elm disease, slime-mold wasting diseases in eelgrass, and sudden oak death syndrome) have been impossible to overlook, even though these have not led to extinctions (Anderson et al. 2004). In contrast, infectious diseases of rare plants are much less studied (Anderson et al. 2004). Moreover, because the majority of known plant extinctions have been among species with very limited geographic distributions, particularly island endemics (IUCN 2004), some of these species may have become extinct as an unnoticed consequence of infectious disease. Because many of the infectious diseases currently threatening endemic plants derive from naturalized species (Anderson et al. 2004), it is likely that infectious diseases have been afflicting insular plant populations at least since humans began in-

roducing exotics to islands thousands of years ago. The rapid increase in the total number of plant species introduced to islands suggests an increasing threat of infectious disease (Atkinson & Cameron 1993). Unfortunately, this remains difficult to evaluate given the paucity of historical data.

Future Directions and Conclusions

Specific knowledge of the individual factors contributing to species extinction and endangerment is critical to the development of efficient and successful conservation strategies. To accomplish this, we must move toward a systematic analysis of the relative effects of the widely proposed causal threats, namely, habitat destruction, overexploitation, invasive species, pollution, and infectious disease (Wilcove et al. 1998). Such analyses must be grounded in sound scientific evidence. As we have shown here, this has been particularly difficult to accomplish for infectious diseases. Indeed, the lack of adequate historical data and the level of uncertainty in existing data make it difficult to gain a veritable understanding of the general role of infectious disease in wildlife extinction and endangerment. Although we can infer patterns of infectious disease threats to wildlife based on theoretical models and the data we have, there is a strong need for improvement in data collection and compilation. We suggest several topics we believe deserve increased recognition and future attention.

First, the lack of historical data make it difficult to support claims that infectious diseases have been emerging at increasingly high rates and are therefore likely to be of significant concern in the future. Alternative indirect methods should not be discounted. For instance, Ward and Lafferty (2004) tracked the proportion of published scientific papers related to infectious disease in several marine taxa to assess whether normalized reports of infectious disease could serve as an indirect proxy for infectious disease monitoring. In the absence of baseline data, this approach is useful for detecting quantitative trends in infectious disease occurrence through time. This and similar methods should prove beneficial for future studies on temporal trends in emerging infectious diseases.

Second, it is crucial to recognize that not all infectious diseases increase the likelihood of extinction. There is a growing need for rigorous scientific tests to determine whether an infectious disease identified in a threatened host causes significant pathology. Related to this is the need to assess whether impacts at the individual level scale up to the population or species level (Lafferty & Holt 2003). Theoretical and historical evidence suggests that infectious disease can drive populations temporarily or permanently to low numbers or densities, predisposing them to extinction by other forces (de Castro & Bolker 2005; Gerber et al. 2005). Infectious diseases that are host

specific and density dependent are unlikely to be the sole cause of species extinction because they typically die out when the host population falls below a threshold density (Anderson & May 1992). Infectious diseases that are frequency dependent, utilize reservoir hosts, or can survive in the abiotic environment are more likely to induce extinction (de Castro & Bolker 2005). Experimental research on the mechanisms of disease-induced extinction will help to clarify the validity of these generalizations.

Third, it is critical that we combine evidence with theory to discern the circumstances under which infectious disease is most likely to serve as an agent of extinction. As described above, this can occur when a pathogen is evolutionarily novel to a susceptible host species, when a pathogen utilizes a reservoir (biotic or abiotic), and when hosts have small pre-epidemic population sizes (de Castro & Bolker 2005; Gerber et al. 2005). Ideally, the combination of evidence and theory can be used to weigh the relative effects and likelihood of such threats to a species' demise, be incorporated into the IUCN's criteria used to assess threat, and thus improve the prioritization of conservation strategies and management efforts. A better understanding of these and other factors that predict risk is sorely needed.

Finally, if a better understanding of the role of infectious disease in species extinction is to be formulated, the ability to detect infectious diseases of conservation concern must be improved by advancing existing surveillance programs associated with economic initiatives and incorporating new ones into ecological research (Aguirre et al. 2002). Accomplishing these four tasks should do much to integrate a science-based understanding of infectious disease dynamics with conservation efforts and ultimately improve our ability to reduce extinctions.

Acknowledgments

This research benefited from conversations with M. Behrens, P. Daszak, S. Gaines, and L. Real. K.F.S. acknowledges funding from a National Science Foundation Graduate Research Fellowship, a Switzer Environmental Fellowship, and a fellowship from the American Association for University Women. K.D.L. benefited from support received from the National Science Foundation through the NIH/NSF Ecology of Infectious Disease Program (DEB-0223565).

Literature Cited

- Aguirre, A. A., R. S. Ostfeld, G. M. Tabor, C. House, and M. C. Pearl, editors. 2002. *Conservation medicine: ecological health in practice*. Oxford University Press, New York.
- Akcakaya, H. R., S. Ferson, M. A. Burgman, D. A. Keith, G. M. Mace, and C. R. Todd. 2000. Making consistent IUCN classifications under uncertainty. *Conservation Biology* **14**:1001–1013.
- Anderson, R. M., and R. M. May. 1986. The invasion, persistence and spread of infectious diseases within animal and plant communities. *Philosophical Transaction of the Royal Society of London, Series B: Biological Sciences* **314**:533–570.
- Anderson, R. M., and R. M. May. 1992. *Infectious diseases of humans, dynamics and control*. Oxford University Press, New York.
- Anderson, P. K., A. A. Cunningham, N. G. Patel, F. J. Morales, P. R. Epstein, and P. Daszak. 2004. Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* **19**:535–544.
- Atkinson, I. A. E., and E. K. Cameron. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology & Evolution* **8**:447–451.
- Berger, L., et al. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America* **95**:9031–9036.
- Butchart, S. H. M., A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. R. Akcakaya, J. E. M. Baillie, S. N. Stuart, C. Hilton-Taylor, and G. M. Mace. 2004. Measuring the global trends in the status of biodiversity: red list indices for birds. *Public Library of Science Biology* **2**:2294–2304.
- Clavero, M., and E. Garcia-Berthou. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution* **20**:110.
- Cunningham, A. A., and P. Daszak. 1998. Extinction of a species of land snail due to infection with a microsporidian parasite. *Conservation Biology* **12**:1139–1141.
- Daszak, P., L. Berger, A. A. Cunningham, A. D. Hyatt, D. E. Green, and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* **5**:735–748.
- Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* **287**:443–449.
- De Castro, F., and B. Bolker. 2005. Mechanisms of disease-induced extinction. *Ecology Letters* **8**:117–126.
- Epstein, P. 2001. Climate change and emerging infectious diseases. *Microbes and Infection* **3**:747–754.
- Gerber, L. R., H. McCallum, K. D. Lafferty, J. L. Sabo, and A. P. Dobson. 2005. Exposing extinction risk analysis to pathogens: is disease just another form of density dependence? *Ecological Applications* **15**:1402–1414.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**:470–474.
- Harvell, C. D., et al. 1999. Emerging infectious diseases—climate links and anthropogenic factors. *Science* **285**:1505–1510.
- Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risk for terrestrial and marine biota. *Science* **296**:2158–2162.
- Holmes, J. C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. *Biodiversity and Conservation* **5**:975–983.
- IUCN (World Conservation Union). 2004. Red list of threatened species. IUCN, Gland, Switzerland. Available from <http://www.iucn.org/themes/ssc/redlist.htm>.
- Lafferty, K. D. 2003. Is disease increasing or decreasing, and does it impact or maintain biodiversity? *Journal of Parasitology* **89**:s101–s105.
- Lafferty, K. D., and R. D. Holt. 2003. How should environmental stress affect the population dynamics of disease? *Ecology Letters* **6**:654–664.
- Lamoreux, J., et al. 2003. Value of the IUCN Red List. *Trends in Ecology & Evolution* **18**:214–215.
- Lederberg, J., R. E. Shope, and S. C. Oaks. 1992. *Emerging infections: microbial threats to health in the United States*. Committee on Emerging Microbial Threats to Health, Institute of Medicine, National Academy Press, Washington, D.C.
- McCallum, H., and A. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. *Trends in Ecology & Evolution* **10**:190–194.

- Possingham, H. P., S. J. Andelman, M. A. Burgman, R. A. Medellin, L. L. Master, and D. A. Keith. 2002. Limits to the use of threatened species lists. *Trends in Ecology & Evolution* **17**:503–507.
- Schorger, A. W. 1955. *The Passenger Pigeon: its natural history and extinction*. University of Wisconsin Press, Madison.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**:1783–1786.
- Van Riper, C., and M. J. Scott. 2001. Limiting factors affecting Hawaiian native birds. Pages 221–233 in M. Scott, S. Conant, and C. Van Riper, editors. *Studies in avian biology: evolution, ecology, conservation, and management of Hawaiian birds: a vanishing avifauna*. Cooper Ornithological Society, Camarillo, California.
- Van Riper, C., S. G. Van Riper, and W. R. Hansen. 2002. Epizootiology and effect of avian pox on Hawaiian forest birds. *The Auk* **119**:929–942.
- Walsh, P. D., et al. 2003. Catastrophic ape decline in western equatorial Africa. *Science* **422**:611–614.
- Ward, J. R., and K. D. Lafferty. 2004. The elusive baseline of marine disease: are diseases in ocean ecosystems increasing? *Public Library of Science Biology* **2**:e120.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* **48**:607–615.

