

Cryptic extinction of a common Pacific lizard *Emoia impar* (Squamata, Scincidae) from the Hawaiian Islands

ROBERT FISHER and IVAN INEICH

Abstract Most documented declines of tropical reptiles are of dramatic or enigmatic species. Declines of widespread species tend to be cryptic. The early (1900s) decline and extinction of the common Pacific skink *Emoia impar* from the Hawaiian Islands is documented here through an assessment of literature, museum vouchers and recent fieldwork. This decline appears contemporaneous with the documented declines of invertebrates and birds across the Hawaiian Islands. A review of the plausible causal factors indicates that the spread of the introduced big-headed ant *Pheidole megacephala* is the most likely factor in this lizard decline. The introduction and spread of a similar skink *Lampropholis delicata* across the islands appears to temporally follow the decline of *E. impar*, although there is no evidence of competition between these species. It appears that *L. delicata* is spreading to occupy the niche vacated by the extirpated *E. impar*. Further confusion exists because the skink *E. cyanura*, which is very similar in appearance to *E. impar*, appears to have been introduced to one site within a hotel on Kaua'i and persisted as a population at that site for approximately 2 decades (1970s–1990s) but is now also extirpated. This study highlights the cryptic nature of this early species extinction as evidence that current biogeographical patterns of non-charismatic or enigmatic reptiles across the Pacific may be the historical result of early widespread invasion by ants. Conservation and restoration activities for reptiles in the tropical Pacific should consider this possibility and evaluate all evidence prior to any implementation.

Keywords *Emoia impar*, Hawaiian Islands, invasive ants, *Lampropholis delicata*, lizard extinction, *Pheidole megacephala*, Scincidae

This paper contains supplementary material that can be found online at <http://journals.cambridge.org>

ROBERT FISHER (Corresponding author) U.S. Geological Survey, Western Ecological Research Center, San Diego Field Station, 4165 Spruance Road, Suite 200, San Diego, California 92101-0812, USA. E-mail rfisher@usgs.gov

IVAN INEICH Muséum national d'Histoire naturelle, Département de Systématique et Evolution, UMR 7205 (Origine, Structure et Evolution de la Biodiversité), CP 30 (Reptiles), Paris, France

Received 17 September 2010. Revision requested 4 November 2010.
Accepted 9 December 2010. First published online 12 March 2012.

Introduction

Extinctions on islands are rampant and have many causes. For reptiles, particularly lizards, insular extinctions greatly exceed those of mainland species and the extinction of smaller lizard species is rarely documented (Case et al., 1991). Incomplete knowledge of island fauna hinders an understanding of the true loss of diversity from these ecosystems, and the issue of morphologically cryptic species also masks quantification of these extirpations or extinctions (Bickford et al., 2007). The Pacific Basin contains the majority of the world's tropical islands. These are most often inhabited by lizards of the families Scincidae and Gekkonidae (Adler et al., 1995; Allison, 1996; Fisher, 1997). Various hypotheses exist for the dispersal of lizards across vast oceanic barriers and these include both natural and anthropogenic processes (Gibbons, 1985; Fisher, 1997; Keogh et al., 2008). We have much less evidence for the extinction of insular lizard populations.

The Hawaiian Islands (Fig. 1) are one of the most isolated archipelagos and have experienced spectacular radiations of their biota, particularly invertebrates and birds (Zimmerman, 1970; Cowie & Holland, 2008). They contain a small lizard fauna that is thought to be of recent origin (McKeown, 1996; Fisher, 1997; Austin, 1999), although this assumption is untested for some skinks (*Cryptoblepharus* and *Emoia*). James et al. (1987; see their Table 1) provided evidence of an early fossil lizard bone that predates humans on the islands, leaving open the question of natural dispersal to the islands. Most of the documented extinctions from the Hawaiian Islands have been from its bird, insect and snail radiations and many hundreds of species are now threatened (Cowie & Holland, 2008). Because of their role in international commercial routes the Hawaiian Islands have experienced major invasions of exotic species; for example, > 2,000 invertebrate species (Howarth, 1985) and many reptiles and amphibians (McKeown, 1996; Kraus, 2002, 2009; Kraus & Duvall, 2004).

Girard (1858) provided the first species list of Hawaiian reptiles but the first detailed study of reptiles was made by Stejneger (1899). Subsequent studies (McGregor, 1904; Snyder, 1917; Tinker, 1941; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; McKeown, 1996) followed and offer a potential history of the appearance and disappearance of species. These data indicate that when Europeans arrived three species of skinks (*Cryptoblepharus poecilopleurus*, *Emoia impar* [as *cyanura* and *schauinslandi*], and *Lipinia noctua*) were present on the Hawaiian Islands.

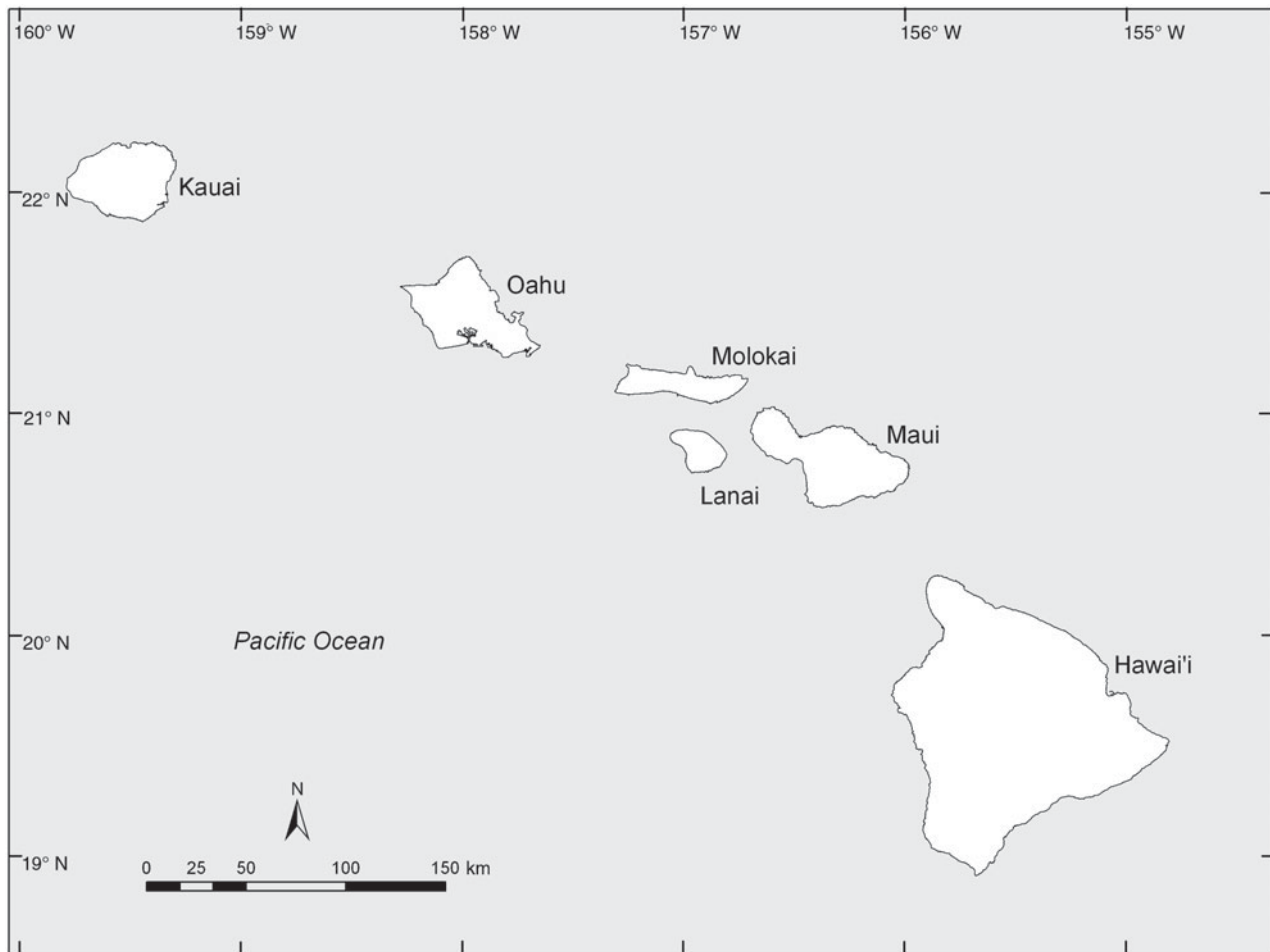


FIG. 1 The large southern islands of the Hawaiian Archipelago. Historical records for *Emoia impar* were documented from all of these islands except Lanai. The invasive species *Lampropholis delicata* has now been recorded from all these islands. The exotic *Emoia cyanura* was only recorded for a limited period of time, from Kauai.

Until recently *Emoia cyanura* was considered a single species across the Pacific Basin but morphological and ecological analysis by Ineich (Ineich, 1987a,b; Ineich & Zug, 1991) indicated that there were two species (*E. cyanura* and *E. impar*) sympatric across this large region. Early recognition that Hawaiian *Emoia* had two distinct forms led Werner (1901) to the recognition of a blue striped one and a melanistic one, although these are colour morphs of the same species. They are members of *E. impar*, and this species is the only *Emoia* species that occurred historically on the Hawaiian Islands. This confusion, and the recent introduction of *E. cyanura*, confounded a full understanding of the history of *Emoia* in the islands. Here we examine literature reports and museum specimens and report field surveys to assess the current status of this genus on the Hawaiian Islands.

Methods

Combining literature and museum data with recent field-work we trace the historical and recent occurrence of *E. cyanura* and *E. impar* across the Hawaiian Islands. We also collected data on the recently introduced *Lampropholis*

delicata (originating from Australia) as part of our assessment of extinction of Hawaiian *Emoia*. The three taxa are ecologically similar as generalist diurnal ground skinks. Of the other skinks, the snake-eyed skink *Cryptoblepharus poecilopleurus* is restricted to rocky or corallian shorelines of the Hawaiian Islands, and the moth skink *L. noctua* is semi-burrowing and semi-arboreal in the Islands.

Literature review

We reviewed all available literature on Hawaiian reptiles, including the main islands and the north-western islands, focusing on *E. cyanura*, *E. impar* and *L. delicata*. We tried to determine the validity of each report of these species and to locate museum specimens vouchering the reports. Data come from both the primary and grey literature.

Museum surveys

We examined *E. impar* and *E. cyanura* specimens in the major museums and confirmed the specific identity of

TABLE 1 Distribution and collecting periods for *Emoia cyanura*, *Emoia impar* and *Lampropholis delicata* on the Hawaiian Islands (Fig. 1). The numbers in the cells represent the number of museum vouchers recorded from that decade.

Species (by island)	Decade of record												Total
	1800–1899	1900	1910	1920	1930	1940	1950	1960	1970	1980	1990	2000	
Hawaii													
<i>L. delicata</i>								1	22	18	15	26	82
<i>E. impar</i>	8												8
Kauai													
<i>E. cyanura</i>										13	1		14
<i>L. delicata</i>						1	1	31	18	6	74	22	153
<i>E. impar</i>		17				1	1	1					20
Lanai													
<i>L. delicata</i>											50	9	59
Maui													
<i>L. delicata</i>							2				17	16	35
<i>E. impar</i>	21	5											26
Molokai													
<i>L. delicata</i>								55		1		18	74
<i>E. impar</i>	14												14
Oahu													
<i>L. delicata</i>		1	5	7	5	107	8	28	29	31	25	49	295
<i>E. impar</i>	11	2											13
No island listed													
<i>E. impar</i>	1												1

Hawaiian specimens. Additionally, we used online collection query tools (Herpnet, Global Biodiversity Information Facility) to determine the presence of additional specimens and, where possible, examined the specimens to confirm identification. Only specimens with detailed island locations are considered. When known, the date of collection is reported in parentheses. See footnote to Appendix for museum acronyms.

Field surveys

We surveyed the historical localities for all reported Hawaiian *Emoia* to determine the current presence of skinks. We used visual encounter transects and random searches. All surveys were during daytime under appropriate weather conditions (sunny or partial clouds). Our fieldwork was conducted on the following islands and years: Kauai, 1988, 1990, 2003, 2008; Oahu, 1988, 2007; Maui, 1988; Hawai'i, 1988, 1990, 2001, 2007, 2008. In addition we consulted other field researchers who may have encountered these species in the field for their observations or additional specimens not deposited in museums.

Results

Literature review

We found literature records (Snyder, 1917) validating the occurrence of *E. impar* from the mid 1800s to 1902. We

could not confirm the presence of *E. impar* after 1902 in any publication. We also found no records for any *Emoia* on the north-western islands and could confirm the occurrence of *Emoia* only from Kaua'i, Oahu, Molokai, Maui and Hawai'i Island (Appendix). *Emoia* have never been reported from any smaller offshore islets.

La Rivers' (1948) general ecological study near the Pearl Harbor area of Oahu in 1944/1945 reported a skink as *E. cyanura*. He encountered only one species of skink. All 1940s Oahu skink voucher specimens (>100) are *Lampropholis*, most from Honolulu and a couple from Pearl Harbor. Thus *L. delicata* was the dominant ground dwelling skink, and he mistakenly identified his specimens as *E. cyanura*. We searched for voucher specimens from La Rivers' study and found none. Oliver & Shaw (1953) discussed *E. cyanura* based in part on their field observations from 1943. They did not indicate that they observed this taxon; their discussion of *E. cyanura* derived from the literature, as did Tinker's (1941). Hunsaker & Breese (1967) surveyed the Hawaiian herpetofauna in 1962 and they do not mention any *Emoia* in the results of their survey. Quay (1973) surveyed several sites on Kaua'i, including the Napali coast, and found only *Lampropholis*.

All subsequent literature reports are clearly not of *Emoia*, except Lazell (1986) who discusses an introduced population of *E. cyanura* that was established in Po'ipu, Kaua'i. McKeown (1996) summarizes the situation with the two *Emoia* species in the Hawaiian Islands and reports the discovery of the *E. cyanura* population at Po'ipu in 1979 by

Matt Walsh. The only museum specimen of *E. cyanura* collected by Walsh (BPBM 8303) is listed as 23 July 1980. Kraus (2005) reported two potential recent records of *E. impar*, one each from Kala'e and Mokapu Islands, both on the north coast of Molokai. Two additional important references are Baker's (1979) discussion of *Lampropholis* history and Bazzano's (2007) surveys of national parks on Hawai'i Island. Neither researcher found *Emoia*.

Museum surveys

Only a few Hawaiian *E. impar* and *E. cyanura* specimens are available in museums. We located fewer than 100 specimens (Table 1; Appendix). There are no *Emoia* voucher specimens from islands north of the main islands; *E. impar* was documented from five of the large islands and *E. cyanura* only from one site on Kaua'i Island. The temporal distribution of the samples shows that only three *E. impar* were collected after 1902, and all 14 *E. cyanura* were collected between 1980 and 1990 (Table 1). *E. impar* records with precise locality came from low elevations (< 300 m; n = 48). It is probable that *E. impar* was present when Europeans arrived and that *E. cyanura* was a recent introduction. Although we did not locate any *Emoia* voucher specimens from islands north of Kaua'i, there are specimens of *E. cyanura* from Wake Island (Atoll) from as early as 1923 (USNM 66829) and these *E. cyanura* are currently still common (J. Helm, pers. comm.). Wake Island is not geographically, geologically, or politically part of the Hawaiian Islands and is thus unrelated to this current discussion.

We located > 700 Hawaiian *L. delicata* in collections. The first record is somewhat confusing; it might be 1909 (BPBM 899; Baker, 1976) although the date is questionable and could be a few years later (P. Imada, pers. comm.). There are several records between 1914 and 1919 from Oahu, thus it was well established by then. The first records for islands other than Oahu are not until the 1940s (Table 1). Within the Hawaiian Islands *L. delicata* occurs from sea level to over 1,000 m. It is the numerically dominant Hawaiian skink in museum collections and now commonly observed in the field.

Field surveys

E. cyanura was observed only on Kaua'i at the Moir Cactus Gardens near Poi'pu and only during our 1990 survey. The specimen collected on that survey is the last one represented in a museum collection. During a 3-day visit in 1990 c. 20 individuals were seen in these gardens. The 2003 and 2008 surveys, conducted at the same site by the same observer (RNF), failed to detect any *E. cyanura*. We suggest that this species is now extinct on the Hawaiian Islands. It probably

occurred on Kaua'i only from the late 1970s to the early 1990s, consistent with available museum voucher specimens. This species never spread outside these gardens. The 1990 sample was included in a genetic assessment of the *cyanura* complex and contained the same mitochondrial haplotype as other populations from the south Pacific, consistent with a recent human introduction to Kaua'i (Bruna et al., 1996a).

In 2008 we searched the three localities on the Napali coast where *E. impar* was last detected on Kaua'i. No *Emoia* were observed, although *Lampropholis* was present, as previously reported by Quay (1973). Other field surveys during other years and on other islands failed to detect any *Emoia* even though they specifically targeted *Emoia* species and the observers had much experience with these lizards elsewhere in the Pacific. This species now appears to be absent from the Hawaiian Islands.

Discussion

Our literature and museum review and recent field work indicate that *E. impar* is now absent from the Hawaiian Islands. The Hawaiian populations were the northernmost occurrence of this species in the Pacific (Ineich & Zug, 1991). Environmental conditions may have restricted it to lower elevations. The temporal pattern of *E. impar* extirpation is striking. They disappeared across all islands by the early 1900s. Museum records demonstrate their presence on multiple islands in the decade between 1892 and 1902. Only three individuals were collected after 1902 (one each in 1948, 1956 and 1963) and all were from within a few kilometres of each other along the remote and rugged Napali coast of Kaua'i, with no records for this species after 1963. These three individuals were collected by different observers and are housed in two collections, indicating that the species persisted along this remote stretch of mountains at least 60 years longer than in the rest of the archipelago.

The extinction of non-charismatic species frequently goes unnoticed, and data are typically lacking to determine the cause. These situations are even more confusing when there are unresolved systematic issues such as those within the *E. cyanura* species complex. Here we have documented the rapid disappearance of a small skink from several islands within the Hawaiian Archipelago in a temporally synchronous pattern. This pattern, and the timing of the extinction, matches that observed for Hawaiian land birds (Atkinson, 1977) and several invertebrate groups (Howarth, 1985; Krushelnicky et al., 2005). This temporal concordance (from the early 1890s to early 1900s) might indicate a single causal factor for these declines. Alternatively, these declines might represent a series of extinctions that were ongoing since Polynesian and European contacts but were brought to the attention of scientists for the first time via the observations of Perkins (1913).

Below we evaluate the main processes that might have caused the extinction of *E. impar*. We highlight the complexity of resolving causation for events that took place a long time ago but are relevant to investigate, as they may inform management and conservation of this and similar species throughout the Pacific.

Habitat destruction

There has been extensive development of the Hawaiian Islands both historically and recently, primarily for cultivation and housing (Burney et al., 2001). Recent research on the south coast of Kaua'i shows that most lowlands of the Hawaiian Islands, including the dry leeward sides, were wetter before humans arrived and contained many species now extinct or restricted to higher, wetter and cooler habitats (Burney et al., 2001). Although this drying has a role in the extinction and endangerment of many lowland species, the Napali coast of Kaua'i (the last known location of *E. impar*) is remote and currently well protected from land-use change. The valleys of this region were historically cultivated but are now regenerated forest habitats.

The introduction of *E. cyanura* onto the Hawaiian Islands was entirely within the Moir Cactus Gardens enclosed within a large hotel complex in Poi'pu on Kaua'i. The habitat is entirely managed and artificial. Elsewhere in the Pacific, *E. cyanura* is often associated with disturbance; *E. impar* typically prefers more forested areas (Ineich, 1987a,b; Bruna et al., 1996b; Schwaner & Ineich, 1998) but both species are often found in syntopy. Low elevation habitat change would affect *E. impar* but it does not alone explain the apparent rapid synchronous extinction of this species across all major Hawaiian Islands.

Competition

The rapid decline and extirpation could result from competition with other skinks. *E. cyanura* was not a competitor as it never spread beyond its point of introduction. Furthermore, it appeared well after the last sighting of *E. impar*. Oliver & Shaw (1953) suggest that the introduction and expansion of *L. delicata* is responsible for declines of *L. noctua*, and this is cited by other authors (Hunsaker & Breese, 1967; Quay, 1973). This assumption derives from the few specimens of Hawaiian *L. noctua* in collections and statements by early collectors on its rarity (although see Tinker, 1941; he apparently confused *L. delicata* for *L. noctua*, stating it was very common, possibly the source of this later confusion). *L. noctua* is uncommonly seen because of its cryptic habits. However, there was little to no temporal overlap between the extinction of *E. impar* and the invasion and spread of *L. delicata*. Perhaps *L. delicata* would have been precluded by *E. impar* or the absence of *E. impar*

allowed *L. delicata* to become established and then to expand across the islands. In 1990 *E. cyanura* and *L. delicata* were sympatric at the Moir Cactus Gardens, and the latter is still present. There is no evidence for competition from other skinks as a cause for the decline and extinction of *E. impar*.

Predation

Both vertebrate and invertebrate predators are widespread on the Hawaiian Islands. Potential vertebrate predators of *E. impar* were reviewed by Atkinson (1977) and Atkinson & Atkinson (2000). Atkinson (1977) provided an accurate and thorough chronology of mammalian introductions as these introductions relate to synchronous bird declines. His assessment was that only the timing of the introduction of ship rats *Rattus rattus* matched the avian declines. The mongoose *Herpestes auropunctatus* and domestic cat (Kirkpatrick & Rauzon, 1986) are both present on the Hawaiian Islands and may have been important in affecting *E. impar*; both prey on small skinks elsewhere in the Pacific (Gorman, 1975; Kirkpatrick & Rauzon, 1986; Bonnaud et al., 2010). The mongoose has been explicitly blamed for the decline of large species of *Emoia* from the main islands of Fiji (Pernetta & Watling, 1978). Atkinson (1977) argued that since the cat was present on Hawaiian Islands prior to the late 1800s it cannot be linked to the increase in bird extinctions later in the century. He also argued that because the mongoose is absent on Kaua'i and Lanai it was not a factor for the synchronous bird extinctions. As it relates to *Emoia*, both cats and mongoose are predators of *E. impar*; however, even where one or both species are present in large numbers, as in Fiji, Samoa, and Tonga, skinks persist although in reduced numbers (Fisher & Ineich, pers. obs.). Regarding the argument for ship rats, they are major predators of birds and skinks (Towns et al., 2006). Atkinson's (1977) argument about the timing of ship rat introductions on Hawaiian extinction thus has merit but the evidence that they could have caused this skink extinction is inadequate. On Clipperton Atoll the stomach contents of rats were examined and few *E. cyanura* were found despite the high density of these lizards and the recent arrival of rats (Lorvelec & Pascal, 2006).

Potential invertebrate predators of *E. impar* are many (Howarth, 1985) but the evidence for ants seems the strongest (Perkins, 1913; Krushelnycky et al., 2005). Ants are well known for causing declines or extinctions of reptiles by various mechanisms, including direct predation of adults or eggs, or indirectly by changing the food available for the reptiles (Mount, 1981; Chalcraft & Andrews, 1999; Fisher et al., 2002; Diffie et al., 2010). The timing of the introduction of the big-headed ant *Pheidole megacephala* and its documented effects on endemic invertebrates gives

credence to their impacts on numerous invertebrate and bird populations (Gillespie & Riemer, 1993; LaPolla et al., 2000; Plentovich et al., 2009). Wetterer (2007) indicated that this ant is common up to 900 m on Hawaiian Islands, well above the elevational limit recorded for *E. impar*, and has been the dominant ant of the Hawaiian lowlands for the last 125 years, often excluding all other ant species (Jones et al., 2001). The early Hawaiian Islands' invasion and dominance of this species into the previously ant-free invertebrate communities may have led to disproportional impacts on species that evolved in the absence of ants (Perkins, 1913). We cannot refute the role of this ant in the decline and extinction of *E. impar*. *L. delicata* evolved in eastern Australia within a rich ant community and is probably not affected by these species in Hawai'i (Andersen, 1995).

Zoonotics

Zoonotics are a possible cause for skink extinction, especially if they were linked to the introduction of *L. delicata*, although there is no temporal overlap of these species on the Hawaiian Islands. Atkinson (1977) discussed the potential diseases of birds that were linked early to their decline. For some native birds, sick and diseased individuals were observed (Perkins, 1913) and disease remains a possibility. The Napali coast and Alakai swamp were also refugia for birds, sharing the same extinction pattern with *E. impar* (Warner, 1968; van Riper et al., 1982).

There is no evidence of mortality among Pacific skinks from virulent pathogens. Externally, *E. cyanura* and *E. impar* of the eastern oceanic Pacific lack parasites (Acari are present on some species in the western Pacific; I. Ineich & R. Fisher, unpubl. data) but there is no evidence of virulence of external parasites in skinks. All preserved specimens from Hawaii lacked external parasites. For internal macroparasites, two recent studies of *Emoia*, both including *E. impar* (Goldberg et al., 2005, 2008), identified several species of cestodes, digeneans and nematodes but it is doubtful that any of these might have become virulent within *E. impar*. Surveys for coccidian species found many new skink coccidians (S.J. Upton, R.N. Fisher, C.C. Austin & D.W. Duszynski, unpubl. data) but there is no evidence that coccidia are virulent in Pacific skinks.

Lastly, malaria is a possible but unlikely cause of the extinction of Hawaiian *E. impar*. Although malaria affects the population density and ecology of lizards there is no evidence of any lizard extinctions from malaria (Schall et al., 1982; Schall, 1996; Eisen, 2001) and no evidence of blood parasites in Hawaiian geckos (Hanley et al., 1995).

If a zoonotic did affect *E. impar*, where did it come from and why does it not affect *L. noctua* and *Cryptoblepharus poecilopleurus*? Since there is no evidence of virulence with

any potential zoonotics it seems unlikely that there was a rapid spread across the islands that led to extinction.

Contaminants

Perhaps early use of chemicals to control mosquitoes or other insect pests caused the widespread declines of *E. impar*. Effects of pesticides and other chemicals are poorly studied in reptiles but recent reviews have identified evidence of some population level effects from modern chemicals although most effects appear to be non-lethal (Todd et al., 2010; Wedding et al., 2010). The extinction of *E. impar* preceded the development of modern chemicals, however, and thus it is unlikely that contaminants were important in its decline. It is possible that the loss of *E. cyanura* from Kaua'i was a result of chemicals used for insect or rodent control in the resort.

Synopsis

We have documented the early extirpation of *E. impar* and the later invasion and expansion of *L. delicata* across the Hawaiian Islands using various forms of evidence. There is, however, no obvious single explanation for the extirpation of *E. impar*. This event appeared to have been rapid, leaving only a small population along a short distance of the Napali coast of Kaua'i into the 1960s. This decline could have been drawn out over many decades, leading to the appearance of being rapid, with only the tail end of the event being documented. The species loss is consistent with the combination of low elevation habitat loss and xerification from human activities (sensu Burney et al., 2001), and the introduction and rapid spread of *P. megacephala* ants throughout the islands. The evidence that exotic mammals, especially rats, caused the rapid extirpation of this species is poor, although their role in affecting lizards is well documented (Towns et al., 2006). Parasites, pathogens and contaminants seem unlikely to have had a major role in the early extirpation of *E. impar* from the islands. The species may still occur on small offshore islands (such as Huelo Islet off Molokai; A. Allison, pers. comm.) as was found for skinks in Guam (Perry et al., 1998) and any detection of the species on the Hawaiian Islands would be an important finding.

The effects of ants on lizards was reviewed by Holway et al. (2002) and there are several examples of ants negatively affecting lizards on tropical islands, including New Caledonia, the Mascarene Islands and the Seychelle Islands (Feare, 1999; Jourdan et al., 2001; Turpin, 2002; Sanchez, 2007; Hansen & Müller, 2009). The recently documented rapid spread of yellow crazy ants *Anoplolepis gracilipes* across Christmas Island and Tokelau has shown how rapidly ants can change island ecosystems and destroy

biodiversity (Abbott, 2006; Sarty et al., 2007; M. Smith, pers. comm.). The early invasion of much of the Pacific Basin by ants and their associated impacts (Krushelnycky et al., 2005) combined with our incomplete knowledge of the biodiversity of this region may have led to many of the observed species disjunctions. Species such as the small skink *Leiopisma alazon*, which is known from one tiny island in Fiji (Zug, 1985), may be currently restricted by ants as early surveys for ants showed invasive species were already present on some of these remote islands before the 1920s (Mann, 1921). Increasing our knowledge of the impacts of invasive ants on vertebrates, particularly lizards, in the tropics should be a priority.

Acknowledgements

We thank the following curators for their help in the loan of specimens in their care: David Kizirian (AMNH), Colin McCarthy (BMNH), Carla Kishinami and Pumehana Imada (BPM), Jens Vindum (CAS), José Rosado (MCZ), Chris Philips (UIMNH), George Zug (USNM) and the late Jens B. Rasmussen (ZMUC). The accomplishment of illuminating the reptile fauna of Hawai'i and the memory of the late Sean McKeown are greatly appreciated by RNF. Allen Allison and an anonymous reviewer offered comments that improved the manuscript, and George Zug provided both substantial encouragement and editing. The use of trade names does not imply U.S. Geological Survey endorsement.

Appendix

The appendix for this article is available online at <http://journals.cambridge.org>

References

- ABBOTT, K.L. (2006) Spatial dynamics of supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, on Christmas Island, Indian Ocean. *Diversity and Distributions*, 12, 101–110.
- ADLER, G.H., AUSTIN, C.C. & DUDLEY, R. (1995) Dispersal and speciation of skinks among archipelagos in the tropical Pacific Ocean. *Evolutionary Ecology*, 9, 529–541.
- ALLISON, A. (1996) Zoogeography of amphibians and reptiles of New Guinea and the Pacific region. In *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes* (eds A. Keast & S.E. Miller), pp. 407–436. SPB Academic Publishing, Amsterdam, The Netherlands.
- ANDERSEN, A.N. (1995) Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation*, 73, 39–43.
- ATKINSON, I.A.E. (1977) Reassessment of factors, particularly *Rattus rattus*, that influenced decline of endemic forest birds in Hawaiian Islands. *Pacific Science*, 31, 109–133.
- ATKINSON, I.A.E. & ATKINSON, T.J. (2000) Land vertebrates as invasive species on islands served by the South Pacific Regional Environment Programme. In *Invasive Species in the Pacific: A Technical Review and Draft Regional Strategy* (ed. G. Sherley), pp. 19–84. South Pacific Regional Environment Programme, Apia, Samoa.
- AUSTIN, C.C. (1999) Lizards took express train to Polynesia. *Nature*, 397, 113–114.
- BAKER, K. (1976) The occurrence and ecological significance of metallic skinks on the islands of Hawai'i and Kaua'i. In *Proceedings of the First Conference in Natural Sciences in Hawaii* (ed. C.W. Smith), pp. 11–18. Hawaii Field Research Center, Hawaii Volcanoes National Park, Hawaii, USA.
- BAKER, J. (1979) The rainbow skink, *Lampropholis delicata*, in Hawaii. *Pacific Science*, 33, 207–212.
- BAZZANO, J. (2007) *Herpetological Inventory in West Hawai'i National Parks: Pu'uuhonua o Honaunau National Historical Park, Koloko-Honokohau National Historical Park, and Pu'ukohola Heiau National Historic Site*. Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa, Hawaii, USA.
- BICKFORD, D., LOHMAN, D.J., SODHI, N.S., NG, P.K., MEIER, R. et al. (2007) Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution*, 22, 148–155.
- BONNAUD, E., MEDINA, F.M., VIDAL, E., NOGALES, M., TERSHY, B., ZAVALA, E. et al. (2010) The diet of feral cats on islands: a review and a call for more studies. *Biological Invasions*, 13, 581–603.
- BRUNA, E.M., FISHER, R.N. & CASE, T.J. (1996a) Morphological and genetic evolution appear decoupled in Pacific skinks (Squamata: Scincidae: *Emoia*). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 263, 681–688.
- BRUNA, E.M., FISHER, R.N. & CASE, T.J. (1996b) New evidence of habitat segregation between two cryptic species of Pacific skinks (*Emoia cyanura* and *E. impar*). *Copeia*, 1996, 998–1005.
- BURNEY, D.A., JAMES, H.F., BURNEY, L.P., OLSON, S.L., KIKUCHI, W., WAGNER, W.L. et al. (2001) Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs*, 71, 615–641.
- CASE, T.J., BOLGER, D.T. & RICHMAN, A.D. (1991) Reptilian extinctions over the last ten thousand years. In *Conservation Biology for the Coming Decade* (eds P.L. Fiedler & P. Kareiva), pp. 157–186. Chapman and Hall, New York, USA.
- CHALCRAFT, D.R. & ANDREWS, R.M. (1999) Predation on lizard eggs by ants: species interactions in a variable physical environment. *Oecologia*, 119, 285–292.
- COWIE, R.H. & HOLLAND, B.S. (2008) Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3363–3376.
- DIFFIE, S., MILLER, J. & MURRAY, K. (2010) Laboratory observations of red imported fire ant (Hymenoptera: Formicidae) predation on reptilian and avian eggs. *Journal of Herpetology*, 44, 294–296.
- EISEN, R.J. (2001) Absence of measurable malaria-induced mortality in western fence lizards (*Sceloporus occidentalis*) in nature: a 4-year study of annual and over-winter mortality. *Oecologia*, 127, 586–589.
- FEARE, C. (1999) Ants take over from rats on Bird Island, Seychelles. *Bird Conservation International*, 9, 95–96.
- FISHER, R.N. (1997) Dispersal and evolution of the Pacific Basin gekkonid lizards *Gehyra oceanica* and *Gehyra mutilata*. *Evolution*, 51, 906–921.
- FISHER, R.N., SUAREZ, A.V. & CASE, T.J. (2002) Spatial patterns in the abundance of the coastal horned lizard. *Conservation Biology*, 16, 205–215.

- GIBBONS, J.R.H. (1985) The biogeography and evolution of Pacific island reptiles and amphibians. In *Biology of Australasian Frogs and Reptiles* (eds G. Grigg, R. Shine & H. Ehmann), pp. 125–142. Royal Zoological Society of New South Wales, Sydney, Australia.
- GILLESPIE, R.G. & RIEMER, N. (1993) The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). *Pacific Science*, 47, 21–33.
- GIRARD, C. (1858) *United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842. Under the Command of Charles Wilkes, U.S.N. Herpetology*. J.B. Lippincott, Philadelphia, USA.
- GOLDBERG, S.R., BURSEY, C.R. & FISHER, R.N. (2005) Helminth records of eleven species of *Emoia* (Sauria: Scincidae) from Oceania. *Pacific Science*, 59, 609–614.
- GOLDBERG, S.R., BURSEY, C.R. & KRAUS, F. (2008) Gastrointestinal helminths of eleven species of *Emoia* (Squamata: Scincidae) from Papua New Guinea. *Journal of Natural History*, 42, 1923–1935.
- GORMAN, M.L. (1975) The diet of feral *Herpestes auropunctatus* (Carnivora: Viverridae) in the Fijian Islands. *Journal of Zoology, London*, 175, 273–278.
- HANLEY, K.A., VOLLMER, D.M. & CASE, T.J. (1995) The distribution and prevalence of helminths, coccidia and blood parasites in two competing species of gecko—implications for apparent competition. *Oecologia*, 102, 220–229.
- HANSEN, D.M. & MÜLLER, C.B. (2009) Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. *Biotropica*, 41, 202–208.
- HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. (2002) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, 33, 181–233.
- HOWARTH, F.G. (1985) Impacts of alien land arthropods and mollusks on native plants and animals in Hawai'i. In *Hawai'i's Terrestrial Ecosystems: Preservation and Management* (eds C.P. Stone & J.M. Scott), pp. 149–179. Cooperative National Park Resources Studies Unit, University of Hawai'i, Honolulu, USA.
- HUNSAKER, D. & BRESE, P. (1967) Herpetofauna of Hawaiian Islands. *Pacific Science*, 21, 423–428.
- INEICH, I. (1987a) *Recherches sur le peuplement et l'évolution des Reptiles terrestres de Polynésie française*. PhD thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France.
- INEICH, I. (1987b) Description d'une nouvelle espèce du genre *Emoia* (Sauria, Scincidae) en Polynésie française. *Bulletin du Muséum National d'Histoire Naturelle. 4e Serie*, 9, 491–494.
- INEICH, I. & ZUG, G.R. (1991) Nomenclatural status of *Emoia cyanura* (Lacertilia, Scincidae) populations in the Central Pacific. *Copeia*, 1991, 1132–1136.
- JAMES, H.F., STAFFORD, T.W., STEADMAN, D.W., OLSON, S.L., MARTIN, P.S., JULL, A.J.T. & MCCOY, P.C. (1987) Radiocarbon-dates on bones of extinct birds from Hawaii. *Proceedings of the National Academy of Sciences of the USA*, 84, 2350–2354.
- JONES, V.P., WESTCOTT, D.M., FINSON, N.N. & NISHIMOTO, R.K. (2001) Relationship between community structure and Southern green stink bug (Heteroptera: Pentatomidae) damage in macadamia nuts. *Community and Ecosystem Ecology*, 30, 1028–1035.
- JOURDAN, H., SADLER, R.A. & BAUER, A.M. (2001) Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonian lizards: evidence from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology*, 38, 283–301.
- KEOGH, J.S., EDWARDS, D.L., FISHER, R.N. & HARLOW, P.S. (2008) Molecular and morphological analysis of the critically endangered Fijian iguanas reveals cryptic diversity and a complex biogeographic history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3413–3426.
- KIRKPATRICK, R.D. & RAUZON, M.J. (1986) Foods of feral cats *Felis catus* on Jarvis and Howland Islands, central Pacific Ocean. *Biotropica*, 18, 72–75.
- KRAUS, F. (2002) New records of alien reptiles in Hawai'i. *Bishop Museum Occasional Papers*, 69, 48–52.
- KRAUS, F. (2005) *Inventory of reptiles and amphibians in Hawai'i Volcanoes, Haleakula, and Kalaupapa National Parks*. Hawaii Biological Survey Contribution No. 2005-013. Bishop Museum, Honolulu, Hawai'i, USA.
- KRAUS, F. (2009) *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis*. Springer-Verlag, New York, USA.
- KRAUS, F. & DUVALL, F. (2004) New records of alien reptiles and amphibians in Hawai'i. *Bishop Museum Occasional Papers*, 79, 62–64.
- KRUSHELNYCKY, P.D., LOOPE, L.L. & REIMER, N.J. (2005) The ecology, policy, and management of ants in Hawaii. *Proceedings of the Hawaiian Entomological Society*, 37, 1–25.
- LAPOLLA, J.S., OTTE, D. & SPEARMAN, L.A. (2000) Assessment of the effects of ants on Hawaiian crickets. *Journal of Orthoptera Research*, 9, 139–148.
- LA RIVERS, I. (1948) Some Hawaiian ecological notes. *The Wasmann Collector*, 7, 85–110.
- LAZELL, J. (1986) The skinks of Poi'pu, Kaua'i. *Journal of Audubon Society*, 46, 155.
- LORVELEC, O. & PASCAL, M. (2006) Les vertébrés de Clipperton soumis à un siècle et demi de bouleversements écologiques. *Revue d'Ecologie (La Terre et la Vie)*, 61, 135–158.
- MANN, W.M. (1921) The ants of the Fiji Islands. *Bulletin of the Museum of Comparative Zoology, Harvard*, 64, 401–499.
- MCGREGOR, R.C. (1904) Notes on Hawaiian reptiles from the island of Maui. *Proceedings of the United States National Museum*, 28, 115–118.
- MCKEOWN, S. (1996) *A Field Guide to Reptiles and Amphibians in the Hawaiian Islands*. Diamond Head Publishing, Los Osos, USA.
- MOUNT, R.H. (1981) The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as a possible serious predator on some native south-eastern vertebrates: direct observations and subjective impressions. *Journal of the Alabama Academy of Science*, 52, 71–78.
- OLIVER, J.A. & SHAW, C.E. (1953) The amphibians and reptiles of the Hawaiian Islands. *Zoologica (New York)*, 38, 65–95.
- PERKINS, R.C.L. (1913) Introduction, being a review of the land fauna of Hawaii. In *Fauna Hawaiiensis*, pp. 15–238. Cambridge University Press, Cambridge, UK.
- PERNETTA, J.C. & WATLING, D. (1978) The introduced and native terrestrial vertebrates of Fiji. *Pacific Science*, 32, 223–244.
- PERRY, G., RODDA, G.H., FRITTS, T.H. & SHARP, T.R. (1998) The lizard fauna of Guam's fringing islets: island biogeography, phylogenetic history, and conservation implications. *Global Ecology and Biogeography*, 7, 353–365.
- PLENTOVICH, S., HEBASHI, A. & CONANT, S. (2009) Detrimental effects of two widespread invasive ant species on weight and survival of colonial nesting seabirds in the Hawaiian Islands. *Biological Invasions*, 11, 289–298.
- QUAY, W.B. (1973) Geographic spread and habits of the metallic skink, *Lygosoma metallicum*, on Kauai, Hawaiian Islands. *Journal of Herpetology*, 7, 308–309.
- SANCHEZ, M. (2007) Observation d'une ponte de *Phelsuma b. borbonica* (Reptilia: Sauria: Gekkonidae) en présence de fourmis exotiques (Hymenoptera: Formicidae). *Bulletin Phaethon*, 25, 24–28.
- SARTY, M., ABBOTT, K.L. & LESTER, P.J. (2007) Community level impacts of an ant invader and food mediated coexistence. *Insectes Sociaux*, 54, 166–173.
- SCHALL, J.J. (1996) Malarial parasites of lizards: diversity and ecology. *Advances in Parasitology*, 37, 255–333.

- SCHALL, J.J., BENNETT, A.F. & PUTNAM, R.W. (1982) Lizards infected with malaria: physiological and behavioral consequences. *Science*, 217, 1057–1059.
- SCHWANER, T.D. & INEICH, I. (1998) *Emoia cyanura* and *E. impar* (Lacertilia, Scincidae) are partially syntopic in American Samoa. *Copeia*, 1998, 247–249.
- SNYDER, J.O. (1917) Notes on Hawaiian lizards. *Proceedings of the United States National Museum*, 54, 19–25.
- STEJNEGER, L. (1899) The land reptiles of the Hawaiian Islands. *Proceedings of the United States National Museum*, 21, 783–813.
- TINKER, S.W. (1941) *Animals of Hawaii: A Natural History of the Amphibians, Reptiles, and Mammals Living in the Hawaiian Islands*. Tongg Publishing Company, Honolulu, Hawaii, USA.
- TODD, B.D., WILLSON, J.D. & GIBBONS, J.W. (2010) The global status of reptiles and causes of their decline. In *Ecotoxicology of Amphibians and Reptiles*, 2nd edition (eds D.W. Sparling, G. Linder, C.A. Bishop & S. Krest), pp. 47–67. CRC Press, Boca Raton, USA.
- TOWNS, D.R., ATKINSON, I.A.E. & DAUGHERTY, C. H. (2006) Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions*, 8, 863–891.
- TURPIN, A. (2002) Un gecko vert de Manapany *Phelsuma inexpectata* victime d'une attaque mortelle de fourmis carnivores. *Bulletin Phaethon*, 15, 56.
- VAN RIPER, C.I., VAN RIPER, S.G., GOFF, M.L. & LAIRD, M. (1982) *The Impact of Malaria on Birds in Hawaii Volcanoes National Park*. University of Hawai'i Cooperative National Park Resources Studies Unit Technical Report no 47. Honolulu, Hawaii, USA.
- WARNER, R.E. (1968) The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor*, 70, 101–120.
- WEDDING, C.J., JI, W. & BRUNTON, D.H. (2010) Implications of visitations by shore skinks *Oligosoma smithi* to bait stations containing brodifacoum in a dune system in New Zealand. *Pacific Conservation Biology*, 16, 86–91.
- WERNER, F. (1901) Ergebnisse einer Reise nach dem Pacific (Schauinland 1896–1897). *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere*, 14, 380–387.
- WETTERER, J.K. (2007) Biology and impacts of Pacific island invasive species. 3. The African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Pacific Science*, 61, 437–456.
- ZIMMERMAN, E.C. (1970) Adaptive radiation in Hawaii with special reference to insects. *Biotropica*, 2, 32–38.
- ZUG, G.R. (1985) A new skink (Reptilia, Sauria, *Leiopisma*) from Fiji. *Proceedings of the Biological Society of Washington*, 98, 221–231.

Biographical sketches

ROBERT FISHER is a research scientist with the U.S. Geological Survey whose research focuses on the impacts of humans on biodiversity. Most of his research is conducted in southern California and the oceanic Pacific. This research involves natural history, historic biogeography, invasive species, and disturbance to determine baseline conditions and current/future impacts to better inform conservation management. IVAN INEICH has been the curator of the squamate reptile collections at the Paris Natural History Museum (MNHN) since 1988. He studies the systematics and biogeography of the reptiles of French Polynesia and has travelled to many Pacific islands and described new lizard and snake species from Vanuatu, Fiji, Micronesia and French Polynesia. His major interests are the systematics, biogeography and conservation of the reptiles of the Pacific islands but he also has an interest in African reptiles.