
THE THREATENED LEOPELMATID FROGS OF NEW ZEALAND: NATURAL HISTORY INTEGRATES WITH CONSERVATION

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Abstract.—Over recent decades, investigators have studied many aspects of the natural history of the threatened and evolutionarily distinct *Leiopelma* frogs of New Zealand, effectively integrating natural history with conservation. To exemplify this, seven aspects of natural history (systematics, senses and defenses, threats, distribution and habitat, reproduction, demography, pathology) are related to 13 conservation needs, and the main linkages identified. This provides both a review of the frogs' natural history and an illustration of their conservation needs. Leiopelmatids have declined markedly and lost species, with three larger species (*L. auroraensis*, *L. markhami*, *L. waitomoensis*) now extinct, and four extant species (*L. archeyi*, *L. hamiltoni*, *L. hochstetteri*, *L. pakeka*) all threatened and on the amphibian EDGE list. *Leiopelma archeyi* tops that list. Potential threats include invasive mammalian predators and emerging diseases, particularly Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*). Distribution surveys have clarified the frogs' current status, extending known ranges of some (i.e., *L. archeyi*, *L. hochstetteri*), and confirming restricted ranges of others (i.e., *L. hamiltoni*, *L. pakeka*). Observations on captive *Leiopelma* clarified patterns of reproduction and development, allowed assessment of evolutionary relationships, and are relevant to captive management of threatened populations. Long-term demographic studies represent some of the most lengthy population research on wild anurans, providing conservation-relevant data, e.g., revealing a decline in *L. archeyi* in the late 1990s, coinciding with finding chytridiomycosis in the species. While *Leiopelma* taxonomy needs more resolution, our knowledge of the natural history of these frogs has substantially informed conservation management, embracing programs dealing with habitat restoration, translocation, adaptive management, captive breeding, and disease prevention.

Key Words.—conservation; frog; *Leiopelma*; natural history; New Zealand

INTRODUCTION

New Zealand has become a world leader in species management because of the precarious status of much of its biodiversity (Bell and Merton 2002; Moore et al. 2008). Part of this biodiversity is the endemic herpetofauna best known for its archaic element (“living fossils”), the Tuatara and Leiopelmatid frogs (Gibbs 2006; Chapple and Hitchmough 2009; King et al. 2009); it is these evolutionarily distinct and globally threatened frogs that I consider here. This paper reflects the focus of Symposium 8 at the 6th World Congress of Herpetology in Manaus, examining the extent to which knowledge of the natural history of these frogs integrates with their conservation. Herman (2002) broadly defined natural history as “the scientific study of plants and animals in their natural environments. It is concerned with levels of organization from the individual organism to the ecosystem, and stresses identification, life history, distribution, abundance, and inter-relationships...” Do we have sufficient knowledge of Leiopelmatid frog natural history to assess species relationships, distributional status, behavior, and ecological requirements? How does such information serve their conservation needs? To address such questions, I illustrate relationships between the frogs' natural history and their conservation through the choice of seven facets of their natural history and 13 areas of conservation need (Fig. 1a).

Systematics.—The Leiopelmatidae of New Zealand belong to the suborder Archaeobatrachia. Their conservative morphology distinguishes them as a family of ancient lineage, and *Leiopelma*, along with *Ascaphus*, comprise the most primitive living anuran genera (Roelants and Bussuyt 2005). Synapomorphies of *Leiopelma* include the presence of ventral inscriptional ribs, low diploid chromosome numbers (18–22), absence of horny beaks in the larvae, and reduction of opercular folds during development resulting in the lack of a closed branchial chamber and spiracle (Stephenson 1955; Green and Cannatella 1993; Bell and Wassersug 2003). *Leiopelma* shares with *Ascaphus* the two defining features of an extra vertebra and tail-wagging (caudalipuboischiotibialis) muscles in the adult (Stephenson 1961).

Darwin (1859) speculated on the unexpected presence of frogs on the relatively isolated landmass of New Zealand. In fact Thomson (1853) reported that gold-diggers found a frog in a creek behind Coromandel town in 1852, and Aitken (1870) reported being shown a native frog from Puriri, near Thames, at about 500 ft (150 m) above sea level. It was not until 1861 that the first species was formally described as *Leiopelma hochstetteri* by Fitzinger (1861). Subsequent species recognized were *L. hamiltoni* (McCulloch 1919), *L. archeyi* (Turbott 1942), *L. auroraensis*, *L. markhami* and *L. waitomoensis* (Worthy 1987a) and *L. pakeka* (Bell et al. 1998a).

Bell.—Conservation of the Leiopelmatid frogs of New Zealand.

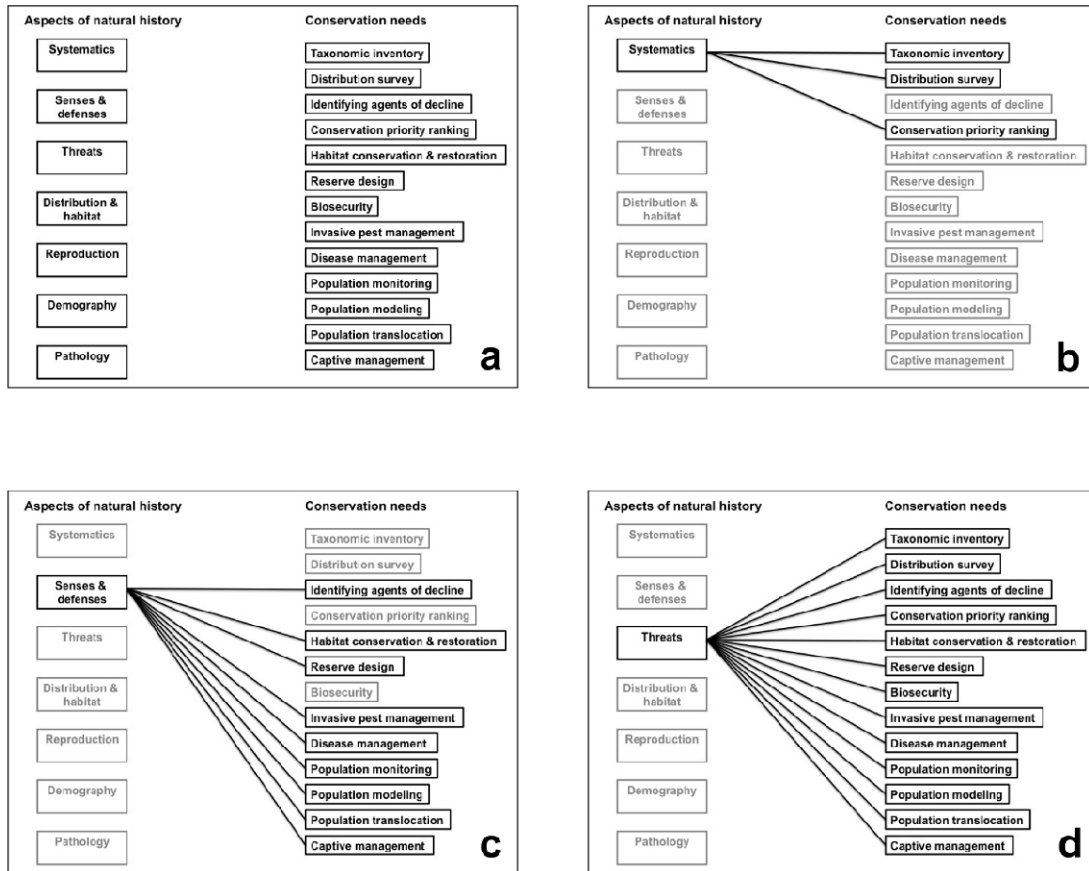


FIGURE 1. (a) To illustrate the links between the natural history and conservation of New Zealand Leiopelmatid frogs, seven aspects of their natural history are related to 13 conservation needs. (b) Main links between systematics and conservation needs. (c) Main links between senses and defenses and conservation needs. (d) Main links between threats and conservation needs.

Leiopelma pakeka, formerly regarded as Hamilton's Frog *L. hamiltoni*, was diagnosed on allozyme and morphometric data (Bell et al. 1998a). Holyoake et al. (2001), though, using partial 12s RNA and Cyt b sequences, have since found little variation between the two taxa (< 1% for Cyt b). They favored keeping them as one species, as has Jewell (2008), though Morris and Balance (2008), Bishop et al. (2009a) and King et al. (2009) retain *L. pakeka*, but recognized that the species status has been challenged. The taxonomy of *Leiopelma*, known as Pekeketua or Pepeketua in Māori, therefore needs more resolution, awaiting further genetic and ecological investigation (Bell et al. 2003; Hitchmough et al. 2007). Indeed naming the New Zealand herpetofauna is an area of continued debate (e.g., Chapple and Hitchmough 2009; Jewell 2009). Studies of *Leiopelma* reveal a broad dichotomy within the genus between four slender species (*L. archeyi*, *L. hamiltoni*, *L. pakeka*, *L. waitomoensis*) and three sturdier species (*L. auroraensis*, *L. hochstetteri*, *L. markhami*; Worthy 1987a,b). Four species are extant (*L. archeyi*, *L. hamiltoni*, *L. hochstetteri*, *L. pakeka*) with their modes of life history and development known (Bell 1978a; Bell et al. 1998a; Bell and Wassersug 2003), but the other three are extinct (*L. auroraensis*, *L. markhami*, *L.*

waitomoensis), described from sub-fossil deposits, and their modes of life history can only be inferred from their skeletal morphology (Worthy 1987a,b). Miocene Leiopelmatid fossils occur in the St. Bathans Fauna in Otago. The size of the vertebrae suggest that they are *L. markhami*, but an isolated vertebra may represent a second frog taxon from one of the more modern anuran families (M.N. Hutchinson, pers. comm.). Bell (1978a) summarized morphological variation in extant species and presented an identification key to adults and larvae. *Leiopelma archeyi*, *L. hamiltoni* and *L. pakeka* are broadly similar in body proportions, but *L. hochstetteri* is more robust, with broader limbs and body but shorter snout and digits. Sexual dimorphism of the forelimbs occurs in *L. hochstetteri*, with the male forelimbs being more muscular, but is not evident in the other species (Bell 1978a). *Leiopelma pakeka* is the largest extant species, reaching 50 mm snout-vent length (SVL), *L. hamiltoni* reaches 46 mm SVL, *L. archeyi* 38 mm SVL, and *L. hochstetteri* 44 mm SVL. Females grow larger than males in all four extant species (Bell 1978a). Genetic studies have revealed that the karyotype in terrestrial species is $2n = 18$, but in *L. hochstetteri* it is $2n = 22$ [$3n = 33$], triploidy being found in some individuals (Green et al. 1984). Moreover, extraordinary variation in the

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supernumerary chromosomes in *L. hochstetteri* and a unique sex determination mechanism by female heterogamety involving a supernumerary univalent W chromosome were reported (Green et al. 1987; Green 1988a). Sharbel et al. (1998) discussed the origin of B-chromosomes in *L. hochstetteri* through sex chromosome devolution. Green and Sharbel (1988) and Green (2002) discussed the comparative cytogenetics of *L. archeyi*, and other *Leiopelma*, reporting a highly differentiated putative W chromosome in a female from Whareorino, though finding the species has less heterochromatin than *L. hamiltoni* [pakeka].

Reflecting the dichotomy among Leiopelmatids, Wells and Wellington (1985) proposed a separate genus (*Leioaspetos*) for the terrestrial *Leiopelma* species, based on comments made by Bell (1978a, 1982a) and Daugherty et al. (1981, 1982); however, the status of the work of Wells and Wellington (1985) was challenged (International Commission on Zoological Nomenclature 1991; Green and Cannatella 1993), and their proposal remains generally unaccepted (see also more general comment by Bortolus [2008]). For practical and conservation reasons, it makes sense to standardize both popular and scientific names for New Zealand frogs, and to resolve outstanding issues of taxonomic debate or uncertainty as far as practicable. This will mostly involve retaining names in current use until new information is available. My interim recommendations (Bell 2007) were to: (1) retain the one genus *Leiopelma* rather than accept *Leioaspetos* for terrestrial species (Wells and Wellington 1985); (2) retain both *L. hamiltoni* and *L. pakeka* as there are fixed genetic differences and morphological differences between the populations; (3) further investigate subfossil *Leiopelma* to clarify relationships between (a) northern "*L. hamiltoni*" subfossils and *L. archeyi*, and (b) the taxonomic status of all mainland "*L. hamiltoni*" (North and South Islands), as discussed by Bell (1994) and Bell et al. (1998a,b); (4) further investigate the *L. hochstetteri* population complex to clarify their relationships and taxonomic status revealed by initial genetic studies (Gemmell et al. 2003; Fouquet et al. 2010); and (5) further investigate Māori names for New Zealand frogs by consulting Māori and reviewing the relevant literature. Not only are the archaic Leiopelmatid frogs of great evolutionary significance but all four surviving species are globally threatened (Hitchmough et al. 2007; the IUCN Red List of Threatened Species, available from <http://www.iucnredlist.org> [accessed 28 February 2009]; Zoological Society of London EDGE: Amphibians, available from http://www.edgeofexistence.org/amphibians/top_100.php [accessed 28 February 2009]). Under the New Zealand threat classification system (Molloy et al. 2002; Townsend et al. 2008), *L. hamiltoni* is classified as Nationally Critical, *L. archeyi* and *L. pakeka* as Nationally Vulnerable, and *L. hochstetteri* as Declining (Newman

et al. 2010). All are in the EDGE list of 'top' 100 amphibians, *L. archeyi* heading that list at No. 1 (Zoological Society of London. 2008. *op. cit.*). Recently Fouquet et al. (2010) identified 13 evolutionary significant units (ESUs) of *L. hochstetteri* that should serve as the focus for future management and conservation of this species, with their New Zealand threat categories ranging from Not Threatened to Nationally Critical (Newman et al. 2010).

Through both their systematic status and their global rarity, these frogs therefore have high conservation value. Different management approaches are required for the two groups (i.e., terrestrial and semi-aquatic), while each species has its own conservation needs (Bishop et al. 2009a). Further molecular and ecological research should help resolve their taxonomy and nomenclature so that the complement of species in New Zealand is better understood, providing improved targets for conservation management. Aspects of their taxonomy mostly relate to three conservation needs: taxonomic inventory, distribution survey, and conservation priority ranking (Fig. 1b).

Senses and defenses.—In *Leiopelma* the visual, tactile, and olfactory senses appear to be particularly important. Whereas they may respond to vibrations and sound, they lack structures seen in other frogs, such as a tympanic membrane, Eustachian tubes, and vocal sacs (Stephenson 1961). Although they can vocalize, as when attacked by a potential predator or when breeding (Bell 1985b), they lack vocal choruses characteristic of many frogs, so population monitoring based on acoustic surveys is impossible. *Leiopelma* species have relatively large eyes (Fig. 2), facilitating nocturnal vision and activity (Bell 1978a, 1982a; Newman et al. 1978; Cree 1989). Based on interspecific comparison of retinal ultrastructure, the eyes of all *Leiopelma* species are principally adapted to operate under low light intensities, but based on its eye, *L. archeyi* would be the least nocturnal species (Meyer-Rochow and Pehlemann 1990). This is consistent with emergence observations, for only *L. archeyi* has been regularly reported as active during the day (Bell 1978a; Cree 1989). This will have



FIGURE 2. *Leiopelma pakeka*, an endangered New Zealand frog that has been studied on Maud Island for over 30 years. (Photographed by Victoria University of Wellington).

implications for field monitoring and for captive management (e.g., feeding regimes in relation to time of day, and light tolerance levels). At night frogs can be located by eye-shine rather than calls. The reflecting tapetum of the eye results in a distinct pinkish eye-shine reflection in a headlamp or torch beam (Bell 1996). Chemical cues may be important in the sensory world of *Leiopelma* species, for example territorial signals. *Leiopelma pakeka* communicates with chemical signals (Lee and Waldman 2002; Waldman and Bishop 2004). This may partly explain the wider dispersion of translocated frogs from a second release at Boat Bay, Maud Island, as olfactory signals from frogs already released there may have deterred the later arrivals from settling among initial colonizers nearer to the release point (Bell et al. 2004b; Trewenack et al. 2007).

Leiopelmatid frogs evolved in an essentially mammal-free environment, but following human settlement New Zealand, they became prey to a wide range of invasive species, including predatory mammals. These have evidently had major impacts on these frogs and other endemic biota (King 1984; Worthy 1987b; Bell 1994; Wilson 2004; Gibbs 2006). Leiopelmatids are generally silent and chiefly nocturnal, so they avoid diurnal avian predators, while spending days in secluded retreats under rocks, logs, or other cover (Bell 1978a). They are also cryptically colored, a further advantage against vision-based predators like birds or Tuatara (*Sphenodon punctatus*). Like many anurans, they have defensive glandular secretions in the skin (Green 1988b) and some of these, such as peptides, have drawn attention in recent research investigating their natural chemical defenses against pathogens (Melzer and Bishop 2009). Also, Leiopelmatids may adopt defensive postures when disturbed or attacked, raising their limbs and holding their bodies in a stiff manner. This was observed in male *L. archeyi*, *L. hamiltoni*, and *L. pakeka* while brooding eggs, but also occurs at emergence sites not associated with breeding (Bell pers. obs.). On handling, some frogs, particularly *L. hochstetteri*, produce frothy secretions (Bell 1985b) around the rear legs, possibly from urine, which may serve a defensive function. When pecked by a New Zealand Robin (*Petroica australis*), *L. pakeka* yelled loudly. This sufficiently deterred the bird to allow escape. The bird then wiped its bill on the ground in a manner reminiscent of removing distasteful skin secretions. A native fish (*Galaxias fasciatus*) and a Tuatara also rejected *Leiopelma* (Bell 1985b). However, a report exists of a Tuatara consuming a *L. hamiltoni* on Stephens Island (Newman 1977).

Translocations are widely used to reintroduce threatened species to areas where they have disappeared (Trewenack et al. 2007). A translocation of *L. pakeka* serves as an example of a continuum multi-species model framework describing dispersal and settling of transferred animals (Trewenack et al. 2007). A variety of different dispersal and settling

mechanisms, which may be density dependent and/or dependent on population-specific pheromonal signals, were considered. When the above model was applied to a case study of a double translocation of *L. pakeka* (Bell et al. 2004b), it suggested that settling occurred at a constant rate, with deterrence from chemical signals probably playing a significant role. This modeling exercise was useful in suggesting design and monitoring strategies for translocations, and was an aid in understanding observed behavior in *L. pakeka*. In conclusion, the senses and defenses of *Leiopelma* relate mostly to nine aspects of conservation (Fig. 1c).

Threats.— The primary threats to *Leiopelma* species include predation by rats (*Rattus* spp.) and Stoats (*Mustela erminea*), both known native frog predators, habitat loss and modification, disease, toxins, climate change, and illegal collection (Bishop et al. 2009a). An introduced frog (*Litoria aurea*) can prey on *L. archeyi*, but the extent of this threat is unclear (Thurley and Bell 1994). Larger invasive mammals, such as Brushtail Possums (*Trichosurus vulpecula*) or feral Pigs (*Sus scrofa*), may affect native frog populations; however, the significance of these introductions as predators and/or habitat modifiers remains undetermined. Feral Cats (*Felis catus*) sometimes prey on native frogs and may be a significant threat as subdivisions adjacent to, or within native frog habitat of *L. hochstetteri* increase (Bell 1994; Thurley and Bell 1994; Newman 1996; Bishop et al. 2009a). The Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*), causing the disease chytridiomycosis, became a newly emergent and significant threat to *Leiopelma* species in the last 15 years (see Pathology section below). It is present in introduced *Litoria* species (Waldman et al. 2001; Carver et al. 2010) and occurs in *L. archeyi* populations in the Coromandel and Whareorino ranges, but not in *L. hochstetteri* (Bell et al. 2004a; Bishop et al. 2009a). Recent proposals to renew mining activity in the habitats of *L. archeyi* and *L. hochstetteri* constitute a further potential threat that arose after the latest assessment of their conservation status had occurred (Newman et al. 2010).

The major factor in the historic decline and extinction of *Leiopelma* species was the arrival of invasive mammalian predators upon human settlement of New Zealand. With Polynesian settlement came the Polynesian Rat or Kiore, *Rattus exulans*, thought to have been a primary agent in species declines (Worthy 1987b). As Wilson (2004) noted “This ostensibly benign little creature ... proved an insidious threat to large invertebrates and small vertebrates.” Many more invasive mammals came with European settlement (King 1984; Wilson 2004), adding to the pressures on surviving endemic frog populations. The Black Rat (*Rattus rattus*) preys on *L. archeyi* (Thurley and Bell 1994; Bell et al. 2004a). The sole survival of *L. hamiltoni* and *L. pakeka* on rat-free islands is circumstantial evidence of their susceptibility to these

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predators (Bell 1994). Preventing colonization by mammalian predators is a management priority for their island habitats. The extent to which invasive predatory mammals had a role in the decline of *L. archeyi* in the Coromandel Peninsula is uncertain (Bell et al. 2004a).

Illegal or accidental introduction of other amphibians to New Zealand poses further potential risks, through competition, predation, or the introduction of pathogens. Such potential biosecurity risks have included the Australian frogs *Lymnodynastes dumerilii* and *Litoria adelaidensis*, the former apparently illegally introduced to the Auckland region in 1999 (Bell 1982a, b; Whitaker and Bejakovich 2000). Egg masses of *L. dumerilii* were reported from the wild, and tadpoles or metamorphs were found in a creek where *Leiopelma hochstetteri* occurred, but were culled by biosecurity agencies (Whitaker and Bejakovich 2000; King et al. 2009).

Conservation threats are approached in many ways in New Zealand, addressing for instance, the need to better identify current agents of decline, to further conserve and/or restore remaining habitats, and to control or eradicate mammalian predators. Given the emergence of disease as a new threat in recent years, more pathology research is required to protect surviving populations. Strict quarantine procedures and anti-predator management are carried out in New Zealand for many *Leiopelma* habitats, especially on islands, or on predator-reduced mainland 'islands', such as the Zealandia sanctuary, Wellington, which is surrounded by a mammalian predator-proof fence (Campbell-Hunt 2002). In conclusion, threats to *Leiopelma* cover a wide range of issues, relating to all 13 areas of conservation selected for review here (Fig. 1d).

Distribution and habitat.—Distribution surveys of extant *Leiopelma* have clarified their current status over recent decades, extending the known ranges of some (*L. archeyi*, *L. hochstetteri*) and confirming the restricted ranges of others (*L. hamiltoni*, *L. pakeka*). Turbott (1942) and Stephenson and Stephenson (1957) provided early information on *Leiopelma* distribution. All extant species of *Leiopelma* have suffered range reductions, and three other species went extinct (Worthy 1987a,b). *Leiopelma hochstetteri*, a semi-aquatic frog, is now the most widespread species, occurring in northern parts of the North Island and on Great Barrier Island (Bell et al. 1985). On Stephens Island, *L. hamiltoni* is confined to a small rock pile near the summit, where the estimated population size is fewer than 300 individuals, so it is among the world's rarest frogs (Newman 1990; Tocher et al. 2006). The extent of available habitat in that area has increased (Brown 1994, 2002), and a translocation to Nukuwaiata Island was initiated in 2004 (Bell 2006; Newman et al. 2010). On Maud Island, *L. pakeka* also has a restricted distribution, but the population is between 19,000–34,000 frogs (Bell and Bell 1994;

Bell 1995; Le Roux 2008; Bell and Pledger 2010). Fifteen frogs, reported as *L. hochstetteri* but possibly *L. archeyi* (Bell 1985b), were transferred to Kapiti Island in 1924–25, but this translocation was evidently unsuccessful (two rat species, *Rattus exulans* and *R. norvegicus*, occurred on the island at the time). A successful intra-island trial translocation of *L. pakeka* to Boat Bay, Maud Island, occurred in 1984–85 (Bell et al. 2004b), and this species has since been translocated to Motuara and Long Islands and to Zealandia (Tocher and Newman 1997; Bell et al. 2004b; Bell 2006, 2008; Lukis and Bell 2007). *Leiopelma archeyi* is the second most widespread species, but its numbers have declined markedly in its former Coromandel ranges stronghold (Bell et al. 2004a). *Leiopelma archeyi* from the Whareorino forest were the subject of an emergency translocation to Pureora forest after chytridiomycosis was discovered in the source population (Bishop et al. 2009a). There are now only two known regions of sympatry among extant *Leiopelma*: between *L. archeyi* and *L. hochstetteri* in the Coromandel ranges and in Whareorino forest (Stephenson and Stephenson 1957; Thurley and Bell 1994; Bell et al. 1998b). Systematic distribution surveys of both native and introduced frogs were initiated in the 1970s (Bell 1972, 1982a) and are now maintained by the New Zealand Department of Conservation, with records now contributing to the Department's Herpetofauna database through the use of Amphibian and Reptile Distribution Scheme (ARDS) cards (Pickard and Towns 1988; Newman 1996; Bishop et al. 2009a). Maps of sub-fossil *Leiopelma* records were provided particularly by Worthy (1987a); as well as, by Bull and Whitaker (1975), Bell (1982b), Bell et al. (1985, 1998a), and Newman (1996). The continued receipt of records of amphibians from all over New Zealand is important for determining their national distribution and for assessing any changes that have taken place over time. No surviving populations of *Leiopelma* are known from the mainland of the South Island, but they could have been there as late as the 1920s and 1930s (Bell 1985b). Searches on the Marlborough Sounds mainland in the 1980s and 1990s failed to find any extant populations (Bell, E.A. 1995. Investigation of the presence of *Leiopelma* frogs and availability of suitable frog habitats in the Marlborough Sounds area. Report for Nelson/Marlborough Conservancy, New Zealand Department of Conservation).

While past declines or extinctions likely resulted largely from the impact of introduced mammals, habitat loss is surely a further contributing factor inducing the range contraction of *Leiopelma* species, especially during the European phase of settlement accompanied by an expansion of agricultural or urban development over much of the country (Bell 1985b, 1994; Bell et al. 1985; Newman 1996). Conservation measures to protect or restore remaining habitats took place for all extant species; however, proposals for further mining activity in Coromandel habitats of *L.*

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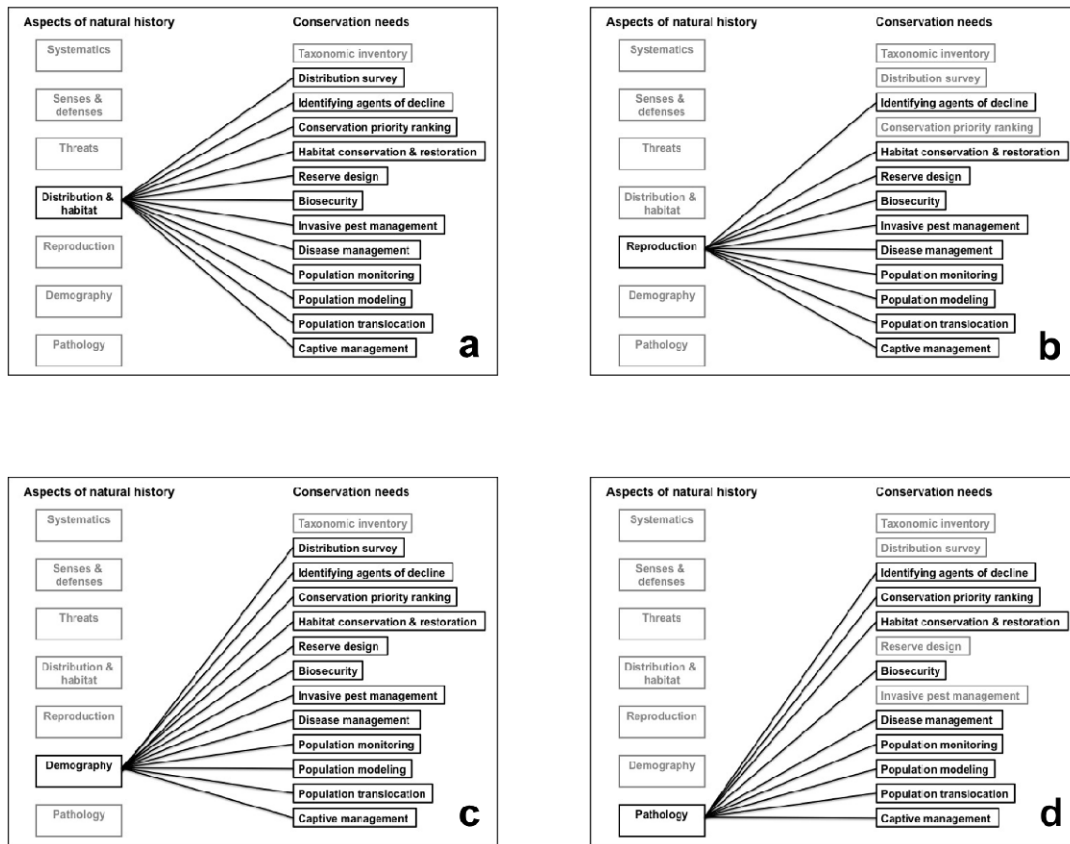


FIGURE 3. (a) Main links between distribution and habitat and conservation needs for the New Zealand Leiopelmatid frogs. (b) Main links between reproduction and conservation needs. (c) Main links between demography and conservation needs. (d) Main links between pathology and conservation needs.

archeyi and *L. hochstetteri* raised national and international concern in 2010 (Bain 2010).

More generally, a clear dichotomy is evident in the habitat choice of the semi aquatic *L. hochstetteri* compared with the three terrestrial species (Crook et al. 1971; Bell 1978; Bell et al. 1985; Cree 1985). Related to habitat choice are physiological adaptations, such as water balance. Cree (1985) examined rates of dehydration, rehydration, and water uptake in response to arginine vasotocin (AVT) in *L. archeyi*, *L. hochstetteri* and (now) *L. pakeka*. She found all three species had high rates of dehydration due to evaporative water loss and urination. This varied inversely and linearly with relative humidity in *L. archeyi* and *L. hochstetteri*. The terrestrial *L. archeyi* and *L. pakeka* rehydrated rapidly and the ventral skin was the major site for water uptake. The semi-aquatic *L. hochstetteri* rehydrated at only one-sixth the speed of the terrestrial species. Rehydration of *L. hochstetteri* was achieved by reducing urine output; there was no obvious change in cutaneous water uptake. These findings have relevance to habitat conservation and to choice of suitable environments for frog translocations, or for captive maintenance, as they have provided information on habitat choice and

physiological differences between species, facilitating their conservation management and recovery. To conclude, information on the distribution and habitats of *Leiopelma* relates to all but one of the conservation needs considered here (Fig. 3a).

Reproduction.—Observations on captive *Leiopelma* have produced new information on breeding behavior, development, and on the evolutionary relationships of *Leiopelma* larvae, with direct relevance to captive management of threatened populations. Using the terminology of Altig and Johnston (1989), the extant species of *Leiopelma* are endotrophic, *L. hochstetteri* being nidicolous, while *L. archeyi*, *L. hamiltoni* and *L. pakeka* are all exoviviparous, hatchlings completing development on the male's dorsum (Bell 1978a,b, 1985a, 2008; Thurley and Bell 1994; Bell and Wassersug 2003). The terrestrial species lay 1–19 eggs in moist depressions on land under rocks, logs, or vegetation; males undertake parental care of eggs and hatchlings (dorsal brooding). The semi-aquatic *L. hochstetteri* lays 10–22 eggs in wet seepages under rocks, logs, and vegetation. Adults usually remain nearby, but intense parental care is absent (Turbott 1949; Bell 1978a, 1982a,b, 1985a). Early embryos of

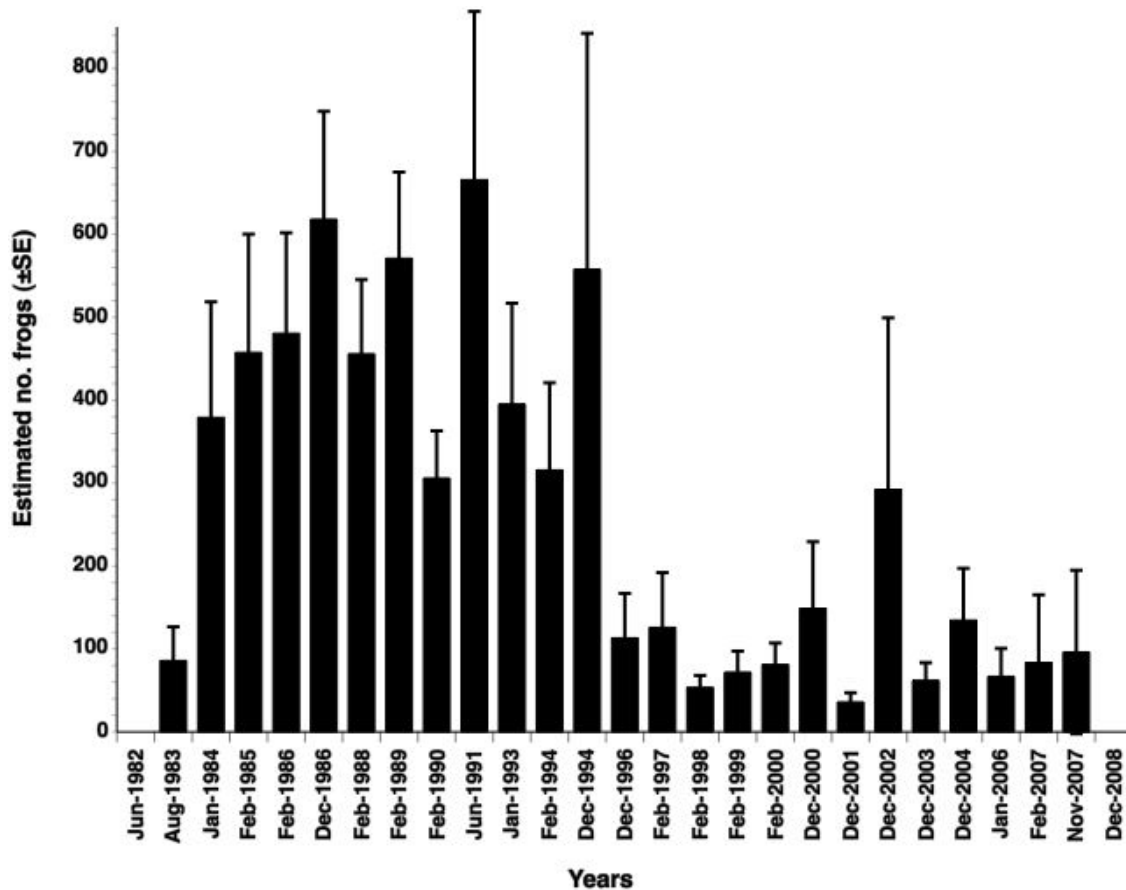


FIGURE 4. A long-term measure of population change (1984–2008): Jolly-Seber estimates of the size of a study population of *Leiopelma archeyi* at a Coromandel Ranges site before and after a marked decline in 1996, that alerted New Zealand conservation agencies to a disease threat (chytridiomycosis). Updated from Bell et al. (2004a).

L. hochstetteri are pale grey on whitish-yellow yolks, while those of terrestrial taxa are whitish on deeper yellow yolks (Bell 1985a). Egg capsules of terrestrial species expand to 10–15 mm diameter prior to hatching, which occurs at a relatively late developmental stage compared with *L. hochstetteri* (ca. Gosner [1960] stage 35–37), although this varies depending on hydrous conditions. At hatching, the eyes are well developed and the body has started to show adult pigmentation. After hatching, young move onto the flanks and dorsum of the male, where they remain relatively inactive. In contrast, egg capsules of *L. hochstetteri* may reach 20 mm in diameter prior to hatching, which occurs at an earlier developmental stage (Gosner stage 27–29), when only eye pigment is distinct. At this stage the hatchlings are mobile and adept swimmers, although typically they remain near the oviposition site during development (Bell 1985a). Larvae of terrestrial species have less developed tail fins, no webbing between the toes, only the bases of the forelimbs covered by the opercular (gular) fold, and a relatively large spherical yolk mass. By having a smaller yolk mass and a longer more muscular tail, *L. hochstetteri* larvae, in contrast, appear more

streamlined and adapted for life in an (albeit shallow) aquatic environment (Stephenson 1955; Bell 1978a, 1982a,b, 1985a; Bell and Wassersug 2003). They also have more pronounced tail fins, the forelimbs being more fully protected by an opercular fold, with toe webbing on both fore and hind feet. In the adult, webbing is retained on the hind feet only.

Breeding in *L. hochstetteri* was noted in the wild by Turbott (1949), while the first captive breeding occurred in 1981 (Bell 1985a). In *L. archeyi*, the pattern of egg brooding was first noted in the wild by Archey (1922), in a species subsequently named after him by Turbott (1942). Successful captive breeding of *L. archeyi* occurred many years later, along with observations of dorsal brooding (Bell 1978a, 1985a; Thurley and Bell 1994). Breeding sites of *L. hamiltoni* and *L. pakeka* are unknown in the wild, but first captive breeding of these species occurred in 1978 and 1976 respectively (Bell 1985a). These captive breeding programs focused on reproductive biology research revealing new information on the breeding pattern of all four *Leiopelma* species (Bell 1985a, 2008). Techniques for ‘fast-starting’ young frogs as a conservation measure now need development,

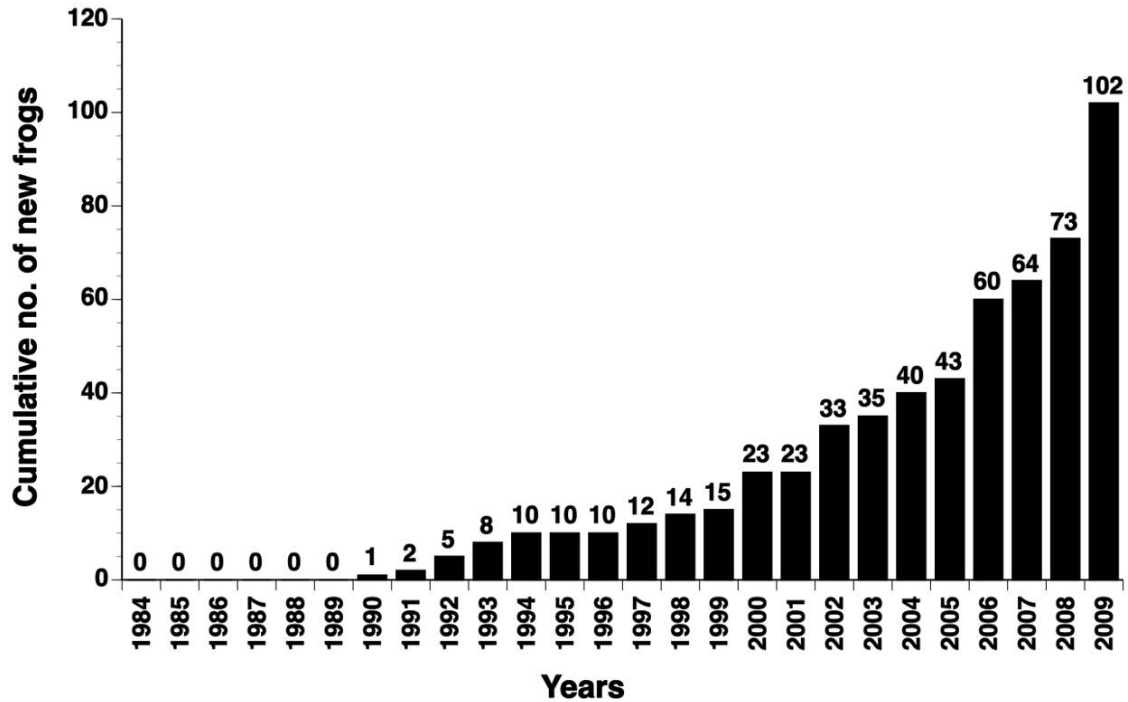


FIGURE 5. Cumulative number of *Leiopelma pakeka* recruits caught after translocation of 100 individuals to Boat Bay, Maud Island, in 1984–85.

although a few young *Leiopelma*, including *L. hamiltoni*, have been reared to adulthood in outdoor enclosures (Bell 1985a). Captive breeding of *L. pakeka* for conservation purposes occurred in Zealandia in 2007–08 and in 2008–09 (Bell 2008, pers. obs.). Developing captive breeding programs is a contingency for populations threatened in the wild, and is part of the draft New Zealand native frog recovery plan (Bishop et al. 2009a). There are many conservation needs directly related to *Leiopelma* reproduction (Fig. 3b).

Demography.—Concern over global amphibian population declines (Stuart et al. 2004; McCallum 2007; Sodhi et al. 2008; Wake and Vrendenburg 2008) highlights the need for more extensive, rigorous monitoring programs because supporting long-term census data are few; so, there are limited opportunities to study changes in numbers and survival over time (Pechmann et al. 1991; Wake 1991; Houlahan et al. 2000; Bailey et al. 2004a,b). Long-term demographic studies of terrestrial *Leiopelma* also integrate directly with conservation, i.e., monitoring temporal changes in abundance. Studies in New Zealand represent some of the most lengthy population research on wild anurans, providing conservation-relevant data on population growth, spatial behavior, survival rate, and longevity, and also revealing K-selected traits with frogs living for up to 37+ years (Bell et al. 2004a,b; Bell and Pledger 2010; Ben Bell, unpubl. data). Population monitoring of *L. archeyi* in its New Zealand stronghold was critical in alerting

conservation agencies to the species' sudden decline in the late 1990s (Fig. 4), coincident with recognition of the species' infection with chytridiomycosis (Bell et al. 2004a). The species IUCN Red List status then changed from Lower Risk (Near Threatened) to Critically Endangered. *Leiopelma archeyi* ranks No. 1 in the world list of Evolutionarily Distinct and Globally Endangered amphibians (Zoological Society of London. 2008. *op. cit.*). Demographic data on *L. archeyi* (e.g., Fig. 4) show numbers did not continue to decline and its New Zealand threat status recently improved from Nationally Critical in 2004 to Nationally Vulnerable in 2009 (Newman et al. 2010). Over 30 years of study on Maud Island provided a substantial mark-recapture database on *L. pakeka*, while a trial intra-island translocation has seen a steady rise in recruitment and population level (Bell et al. 2004b; Fig. 5). The need for sustained and robust amphibian monitoring has therefore been met through long-term studies of the terrestrial *Leiopelma* frogs (Newman 1990; Bell et al. 2004a,b; Tocher et al. 2006; Pledger and Bell 2008), although long-term demographic study of *L. hochstetteri* is vital too. Demographic aspects of natural history relate to most conservation needs of *Leiopelma* species (Fig. 3c).

Pathology.—As the decline of *L. archeyi* in the Coromandel ranges (Fig. 4) coincided with recognition of the species' infection with chytridiomycosis (Bell et al. 2004a), research on disease pathology increased markedly in New Zealand and involved veterinarians, conservation managers, and herpetologists. This led to

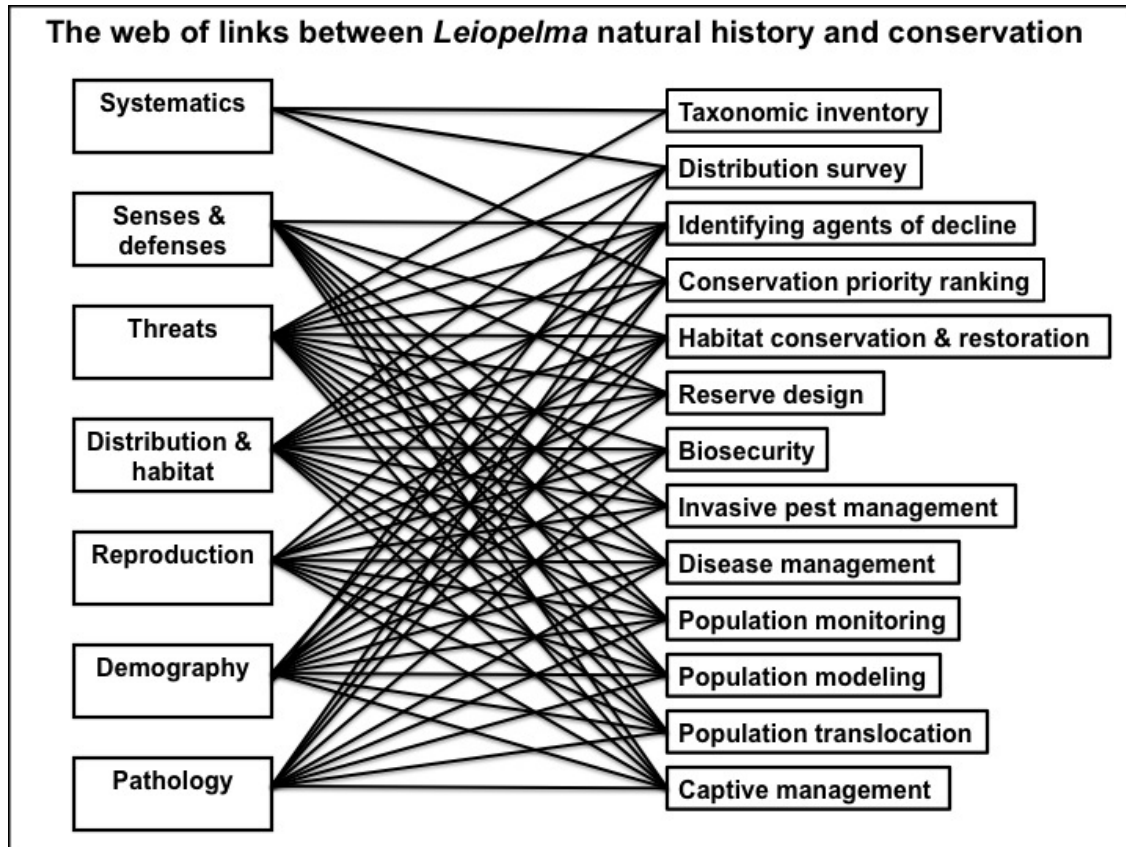


FIGURE 6. The web of links between natural history and conservation needs for the New Zealand Leiopelmatid frogs.

instigation of hygiene protocols for frog research and management (Bishop et al. 2009a). On Maud Island, for instance, protocols for *L. pakeka* research include keeping most equipment on the island, quarantine checks and disinfecting all equipment carried to the island, disinfecting and cleaning clothing, wearing rubber gloves when handling frogs, and isolation (non-mixing) of any frogs caught. The control of infectious disease is a challenging management issue (Bell et al. 2004a; Hansford 2004). Amphibian Chytrid Fungus now infests *L. archeyi* throughout its known range, including study populations in the Coromandel and Whareorino ranges. We know of no other afflicted species, despite *L. hochstetteri* occurring sympatrically on ridges and under forest with infected *L. archeyi* (Bell et al. 2004a; Bishop et al. 2009a). Swab samples of *L. pakeka* on Maud Island in 2006 and 2008 (each of 30 frogs) were negative, although the ‘Sword of Damocles’ may still hang over both *L. pakeka* and *L. hamiltoni*, morphologically and ecologically similar to *L. archeyi* (Bell 2002; Bell et al. 2004a,b). Translocations to other sites should further lessen the risk of disease striking these island species. The evidence suggesting that disease could be a major agent of decline in *L. archeyi* from the Coromandel ranges is: (1) the rapidity and severity of decline; (2) the progressive (south to north) nature of decline; and (3) occurrence of frogs with chytridiomycosis

simultaneous with the decline (Bell et al. 2004a). Sympatric populations of the semi-aquatic *L. hochstetteri* remain relatively stable. Even the population of *L. archeyi* in the Whareorino forest remains stable, despite the co-occurrence of chytridiomycosis at that location.

Of 57 *L. archeyi* from the Coromandel ranges study site over 2006–2010, 8–10 (14–18%) tested positive for chytridiomycosis when using real-time polymerase chain reaction analysis. Bell et al. (2004a) reported more smaller individuals lost following the population decline; whereas, during 2006–2010 the mean snout-vent length (SVL) of 10 infected frogs (28.1 mm) was just significantly less than for 47 uninfected frogs (31.9 mm; $t = 2.036$, $df = 55$, $P = 0.047$). Over this period, infected frogs appeared superficially healthy, and their survival and condition was monitored. One of the frogs (SVL 20–23 mm) tested positive for the disease in 2007, and again 13 months later in 2008, but appeared healthy. Six others (all probable females, SVL 32–37 mm) tested negative for the disease on successive captures 1–2 years apart.

Amphibian Chytrid Fungus was eliminated by *L. archeyi* in clinical trials: 11/12 frogs (92%) cleared their infection within three months of capture, and the infection in the remaining frog was eliminated using topical treatment with chloramphenicol, with no apparent acute adverse reactions (Bishop et al. 2009b).

Despite this promising result, sustaining and restoring populations of *L. archeyi* in New Zealand raises major challenges for conservation management. The disease and population status of *L. hochstetteri* needs to be investigated further, as does the extent of genetic and taxonomic diversity across its present range of distribution (Green 1994; Gemmel et al. 2003; Fouquet et al. 2010). Clearly, the pathology of *Leiopelma* needs further research, and this area of their natural history again relates to many areas of conservation (Fig. 3d).

Conclusion.—Do we have sufficient knowledge of the natural history of Leiopelmatid frogs to enable informed assessment of species relationships, distributional status, behavioral, and ecological requirements? Do we know how these factors might influence their conservation and management? I believe so, to a fair extent. Our knowledge of the natural history of these frogs has provided for informed conservation management that embraces programs dealing with habitat restoration, translocation, adaptive management, captive breeding, and disease prevention. The aspects of natural history reviewed here impact many to all of the 13 conservation needs that we considered. The extent of relationships is vividly summarized and illustrated by the web of links between natural history and conservation needs (Fig. 6). I therefore conclude that there is abundant evidence of close integration between the natural history of the threatened New Zealand Leiopelmatid frogs and the needs of their conservation, but I recognize that much more research must be done, particularly to improve captive management, to unravel species relationships, and to determine the impact and control of disease and predators.

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