


special issue:

Feathers to Fur

The ecological transformation of Aotearoa/New Zealand



Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history?

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Abstract: Pre-human New Zealand had some unusual feeding guilds of birds (e.g. the herbivorous moa fauna), thought to have developed as a result of the absence of a 'normal' mammal fauna. Insectivorous birds, on the other hand, are an integral part of all the world's ecosystems, regardless of the presence or absence of mammals. While it is acknowledged the overall predation impact from birds in New Zealand is unlikely to have differed greatly from elsewhere, the low impact of mammalian insectivores (apart from microbats), coupled with the presence of a specialised avian feeding guild that concentrated on ground-active prey, might have exerted certain unique selection pressures. Do New Zealand invertebrates reflect this? It would be necessary to compare the New Zealand invertebrate fauna with that of mammal-dominated lands in greater detail than is available today before we could assert whether any unique anti-predator characteristics have evolved. Knowledge of the insects that succumbed to extinction when mammals invaded New Zealand should provide clues to avian-adapted features that might have rendered them particularly vulnerable to introduced rodents. Predation by kiwi (*Apteryx* spp.), an extraordinarily mammal-like nocturnal bird, may to some extent have prepared the invertebrate fauna for the arrival of small mammals.

Keywords: anti-predator defenses; camouflage; extinctions; insect ecology; island ecology; large body mass; vertebrate predation

Introduction

New Zealand has been described as 'a completely different experiment in evolution from the rest of the world' (Flannery 1994: 55), an isolated archipelago where birds ruled in the absence of mammals. These are the widely accepted visions of pre-human New Zealand. Over the past 800 years, the geographical barriers have been broken and human colonisation has 'rectified' the absence of mammals. The result has been a clear demonstration of the impact of mammals, even very small ones, on an unprepared fauna and flora (Wilson 2004; Innes et al. 2010; Tennyson 2010). In 1986, the New Zealand Ecological Society held a special symposium which examined the role of the moa (*Aves: Dinornithiformes*) fauna and the subsequent impact of alien mammals on vegetation and landscapes. The 'Feathers to fur' symposium in 2007 (Sullivan et al. 2010) was intended to update our interpretation of the wide ranging changes which took place when a bird-dominated ecosystem became invaded by mammals, and thus extend the scope of the first symposium and address the question of what was driving those changes.

In 1986, the major debate focused on whether moa herbivory or Pleistocene climate was the selective force behind New Zealand's abundance of divaricating plants (Atkinson &

Greenwood 1989). Since that time, this speculative moa-driven scenario has been steadily reinforced by subsequent studies (e.g. Bond et al. 2004; Lee et al. 2010; but see McGlone et al. 2010), to the point where it is now fairly well accepted that the unique impact of moa herbivory, in lieu of mammalian herbivory, has driven the evolution of certain special features of the New Zealand flora. Examples include the juvenile lancewood growth-form, the spiny-leaved *Aciphylla*, and the divaricating plant syndrome. Biologists have also given attention to the possible roles of avian predators in the evolution of anti-predator responses in the New Zealand fauna (Worthy & Holdaway 2002), with the realisation that what changed when mammals arrived was not a question of the sudden impact of predation where there had been none before, but rather a switch from avian to mammalian predators and all that implied (Holdaway 1989; King 1984; Kelly & Sullivan 2010). For example, behavioural (e.g. 'freezing' as an anti-predator response) and morphological (e.g. cryptic colouration) adaptations have been recognised in the New Zealand avian fauna; such adaptations would have served to protect some birds from their avian predators (raptors) (Elliott et al. 2001). The question of whether parallel responses can be detected in the invertebrate fauna has not been addressed. This paper presents a preliminary discussion of how we might

go about investigating this. Can we identify any features of New Zealand's invertebrate fauna that might distinguish it from the faunas of 'normal' mammal-driven locations? What was unusual about the predator fauna of pre-human New Zealand? And can we learn anything from the results of mammal introduction when humans ultimately terminated the 'mammal-free' status?

Was New Zealand predation different?

In order to address the question of whether any New Zealand invertebrates differ from those of other lands as a result of evolution with birds in the absence of mammals, we need to first examine the nature of the vertebrate fauna that influenced this country's invertebrates. If we can accept the avian-driven evolutionary scenario for divaricating plants (Atkinson & Greenwood 1989), then perhaps we are ready to extend that avian influence to insects and other invertebrates. However, with invertebrates, we can reasonably assume that the avian impact was through direct predation rather than through any indirect influence on plant life. Hence the most notable of all of New Zealand's unique birds, the herbivorous moa guild, is unlikely to have had any direct influence on the nature of the invertebrate fauna. We must look to other feeding guilds of birds in pre-human New Zealand.

Atkinson and Millener (1991) reconstructed the feeding guilds of New Zealand birds based on the Holocene fossil record. Apart from the large ground herbivores (moa) that had no such extensive counterpart elsewhere, they also identified a ground-surface/subsurface feeding guild of ground insectivores which raked, dug, probed and gleaned for invertebrates on the forest floor, claiming that such a guild was not represented elsewhere. This group includes the kiwi species (Apterygiformes: *Apteryx*), flightless rails (e.g. weka (Gruiformes: *Gallirallus*), snipe (Charadriiformes: *Coenocorypha*), snipe-rail (Gruiformes: *Capellirallus*), owl-nightjar (Caprimulgiformes: *Aegotheles*), acanthisittid wrens (Acanthisittidae) and robin (Petroicidae: *Petroica*), together with the laughing owl (Strigiformes: *Sceloglaux*) and the enigmatic *Aptornis* (Gruiformes: Aptornithidae), a total of seventeen species, nine of which are extinct. Thirteen were flightless or had reduced powers of flight, and at least eight were nocturnal or crepuscular. Apart from kiwi, which must be rated as unique in this context, some components of this guild may well have existed elsewhere, such as blackbird and thrush (*Turdus* spp.), but they would have been less nocturnal in their feeding impacts. On the other hand, the guild of 20 arboreal (and presumably diurnal) insectivores, although containing some unique examples like huia, was not exceptional in terms of foraging behaviour or sensory mechanisms. They point out that elsewhere, for example in Australia, the diurnal insectivores are also predominantly birds, but in contrast with New Zealand, there is a paucity of ground-feeding insectivorous birds, their place being taken by nocturnal insectivorous marsupials (Lein 1972). New Zealand's ground-active lizard fauna, in the absence of mammalian competition and predation, might also have fulfilled the roles of some insectivorous mammals elsewhere.

Identifying the characteristics of predator-avoidance in invertebrates

Unfortunately, we cannot study the characteristics of the Quaternary invertebrate fauna in the kind of detail that exists for the vertebrate fauna, simply because the fossil evidence does not exist. The bottom line, as it was for the ill-prepared

vertebrate fauna, was extinction of many invertebrates when the first mammals entered their domain. This research area has suffered from both a lack of material and a lack of researchers and there is scattered information only. As an alternative, we must examine the contemporary invertebrate fauna, seeking characteristics that may be especially well developed in the New Zealand fauna, but not present in equivalent overseas faunas. We must ask whether any distinctive characteristics could be related to the dominant avian influence.

For an invertebrate, longevity is usually a matter of avoiding predation, so it follows that characters that confer anti-predator advantages should be selected for. It is generally agreed that birds (except kiwi, see below) hunt their prey differently from mammals, using highly developed visual senses, but lacking the sensitive olfactory skills of mammals (Worthy & Holdaway 2002). Ideally, what is needed is a comparative review of the incidence of invertebrate anti-predator attributes in the New Zealand fauna in relation to more 'typical' locations elsewhere. Fortunately, a twenty-year literature review of anti-predator mechanisms in arthropods (Witz 1990) has provided a list of 16 possible strategies, 12 of which are included in Table 1, together with three I believe apply particularly to the New Zealand situation. I will use this revised list of strategies to summarise what I believe to be the six main characteristics for comparison between the New Zealand fauna and an invertebrate fauna that has long co-existed with both mammal and bird predators (i.e. a 'normal' vertebrate fauna). These are: (1) colouration; (2) body size and flight loss; (3) odour; (4) habitat partitioning and day-night activity; (5) escape reactions; and (6) taxonomic representation.

(1) Colouration

Insects and other invertebrates that commonly spend time at rest on exposed surfaces like leaves, stems or flowers, or on the ground, are generally renowned for their cryptic appearance in terms of colour, outline and ornamentation. Cryptic features will apply to both diurnal and nocturnally active forms. A dominant presence of mammalian insectivores (with their good olfactory skills) might conceivably downgrade the value of crypsis, whereas a dominance of birds or reptiles might lead to a greater than expected proportion of cryptic invertebrates. What can we conclude about New Zealand invertebrates? While the insect fauna certainly gives the impression of supporting this contention, particularly in comparison with more tropical lands, I hesitate to proclaim it without undertaking detailed comparative analysis. It is true that overseas visiting entomologists can be heard to remark how drab and depauperate the New Zealand fauna is, until they see the full diversity revealed through the aid of a light trap or other type of lure. If such a degree of crypsis can be substantiated by proper analysis, then this is surely an excellent example of avian-driven evolution. Of course, cryptic invertebrates occur everywhere, so the distinctions are going to be matters of degree. Carrying the crypsis speculation further, we might expect to see certain behaviours in an unusually high proportion of the cryptic species, e.g. tendencies to avoid taking flight by day and to be active on the ground at night. In these situations avian predators would be at a distinct disadvantage (see 4 below).

Less readily explained is the extreme rarity of mimicry and conspicuous warning colours in the New Zealand invertebrate fauna. These conspicuous signals might be expected to proliferate under the influence of diurnally-active, visually-proficient predators.

Table 1. A list of potential predator-avoidance characteristics in invertebrates with an indication of their significance in New Zealand (loosely based on Witz 1990). For the purposes of this table, the New Zealand incidence is recorded from personal assessment, rather than a comprehensive literature survey.

Category	Explanation	Significance in New Zealand
Crypsis	Colour or behaviour	High – a prominent feature noted by visiting entomologists – phasmids, moths, beetles, grasshoppers,
Body size	Vertebrate predators select for large size	High – large body-size targeted by mammals that invaded New Zealand
Chemical	Defensive secretions and odours	Moderate – notable in ground beetles, centipedes, wētā
Habitat and day/night partitioning	Ground or canopy active; diurnal or nocturnal	Moderate – invertebrate activity zone/time determines which avian feeding guild will impact on them
Use of protected refuge	Hole or crevice-seeking to escape predation	Moderate – refuge seeking behaviour has high value in avian-dominated ecosystem, acts as ‘pre-adaptation’ for small mammals (tree wētā)
Escape	Detection of predator – rapid escape	Moderate – surviving invertebrates show responses to rat predation pressure
Feigning death	Lack of movement	Moderate – likely to be of high survival value under avian or reptile predation, seen in some beetles, moths
Acoustic	Noise, stridulation	Low but present – wētā, longhorn beetles
Fighting	Biting, stinging, kicking, display	Low – but adopted by wētā. May be significant for lizard predation.
Armour	Spines, horns	Low – wētā, a few beetles
Warning	Colour, behaviour	Low – a few flies
Mimicry	Colour or behaviour	Very low
Misdirected attack	Eyespots, false heads – predator attacks less vulnerable part	Very low
Saturation with numbers	Swamping effect of large numbers	Low – chorus cicada
Mutualism	Another organism assists	Not recorded in New Zealand

(2) Body size and flight loss

An increase in body size, coupled with loss of flight, is widely accepted as a feature of the (now largely extinct) New Zealand avian fauna which developed in the absence of mammals. Have invertebrates been affected in the same way? Certain New Zealand examples are frequently cited in this context, namely carnivorous paryphantid landsnails, giant wētā, and possibly athoracophorid slugs (Atkinson & Millener 1991). However, these examples, although clearly large and flightless, and the numerous flightless beetles (weevils, stag beetles, carabids) and phasmids (Watt 1975; Atkinson & Millener 1991), have their equivalents on most other southern landmasses, where they co-exist with mammals. One group highlighted by Watt was the giant wētā (*Deinacrida*) which have been claimed to occupy the niche of small rodents (Ramsay 1978b). The fact that lowland species of *Deinacrida* have become extinct on mainland New Zealand since the introduction of rodents (see below) suggests these large insects might well qualify as bird-driven forms that are unique to New Zealand. But, before we become too readily convinced by this argument, we should consider the presence of similar large-bodied ground-surface orthopterans in Australia and other lands, in the presence of mammals, which suggests perhaps it is more some feature of their behaviour that makes them vulnerable, rather than size and flight loss per se (Gibbs 1998). New Zealand’s flightless terrestrial beetle fauna is not remarkable by world standards, yet some have succumbed to rodent invasions (discussed below) while others have survived.

It is worth noting that the unique ground-feeding guild of avian predators did little to suppress the rich diversity and

abundance of small litter-dwelling arthropods and mollusks; their diversity is as high as the maximum diversity recorded anywhere in the world, even today in the presence of introduced mammals (Barker 2005).

(3) Odour

Pheromone communication is almost universal in insects. It goes with a nocturnal lifestyle and highly specialised chemosensory detectors. In most instances, the volatile chemical components are so subtle they are undetectable, except by the intraspecific recipient. However, in some cases, the odour is so pungent that even a human becomes aware of it. In New Zealand, the acrid smell of tree wētā secretions is well known. The musky smell of kakapo (a parrot) has been highlighted as an example of a characteristic odour that would be unlikely to confer any penalty in an avian-dominated world, yet it would become highly deleterious in the presence of carnivorous mammals with their acute sense of smell (Worthy & Holdaway 2002).

The giant wētā species that were rapidly extinguished by rodents on mainland New Zealand (e.g. *Deinacrida heteracantha*, *D. rugosa*), are overt pheromone communicators but they lack the behavioural attribute of seeking safe refuges when not out foraging (Gibbs 1998). It seems highly likely that, like kakapo, these wētā developed their use of strong odour in an avian-driven ecosystem where the use of such chemicals was no threat. The vulnerable wētā (*Deinacrida* species) contrast with the successful ‘street-wise’ tree wētā species (e.g. *Hemideina thoracica* and *H. crassidens*) which, despite their reliance on powerful odours, still thrive in modern mammal-invaded New

Zealand as a result of their 'pre-adapted' behavioural responses (see 5 below) and the use of secure refuges (Gibbs 1998). Although both types of wētā conform to the large-bodied, flightless syndrome, tree wētā exemplify the importance of these avian-mediated behavioural adaptations that can function just as efficiently against mammals. The example contrasting *Deinacrida* and *Hemideina* wētā illustrates the difficulty of making generalisations based on morphological attributes.

Although not the case with wētā species, strong odours may be associated with a warning signal, as they are in the carabid beetles, also large-bodied and flightless, with ground-surface activity. Carabid beetles occur world-wide and are successful, with or without mammalian insectivores, because their odour is associated with a defensive secretion, effectively warning predators of their distasteful properties.

(4) Habitat partitioning and day-night activity

In a 'balanced' vertebrate predator community where both mammals and birds coexist, we might expect mammals to predominate on the ground surface, with birds far exceeding mammals in the arboreal zone (except at night). Thus, we should look on the ground for avian-driven distinctions. As we have seen, a unique insectivorous ground-active bird guild was able to evolve in New Zealand in the absence of mammals (except for bats). With their differing prey-detection senses, it is conceivable this avian guild selected for certain invertebrate characteristics that then placed these taxa at risk once ground-active mammals invaded. Elucidating these characteristics would be extremely difficult. However, we could approach this question in a more generalised way, by asking whether there is any evidence that New Zealand invertebrates show a higher level of nocturnal ground-surface activity than one would find in equivalent situations elsewhere. It would be a challenge to tackle such a question and it would need to be conducted in a 'pristine habitat' where introduced small mammals have not already eliminated the very invertebrates that could illustrate the point. The hypothesis would be that New Zealand's forest-floor community of invertebrates exhibits a greater degree of nocturnal surface activity than would occur in an equivalent habitat elsewhere. By 'surface activity' I am referring to both fully exposed and sub-surface litter-dwelling invertebrates. It follows also that we would expect no distinctive features in the arboreal arthropod communities since, wherever they occur, these communities are dominated by avian predators.

The potential impact of kiwi species on ground-surface invertebrates deserves a mention, since no other bird occupies the same niche. Kiwi are an exception to the general bird syndrome, being nocturnal with poor eyesight but a highly developed sense of smell and movement (Martin et al. 2007), thus functioning very like a mammal. With what must have been large numbers of nocturnally-active kiwi, as well as snipe-rails and weka, the invertebrate fauna is likely to have experienced pressures remarkably akin to a situation with insectivorous mammals.

(5) Escape reactions

Survival of an invertebrate often depends on early detection and rapid avoidance of a predator. The use of refuges that provide protection from predators can be an integral part of this behaviour. Bremner et al. (1989) investigated the behavioural reactions of invertebrates on Fiordland islands, with and without mammalian predators. They found that the escape responses of cockroaches (*Celatoblatta notialis*), jumping wētā (*Isoplectron* sp. and *Talitropsis* sp.) and web spinning spiders on islands

with rodent predators were significantly more pronounced than on predator-free islands. In other words, their threshold of stimulation required to elicit escape responses had decreased in the presence of rodents.

In another case, behavioural adaptations of tree wētā (*Hemideina crassidens*) from rat-infested and rat-free habitats, were tested in a series of identical experimental cages in which wētā behaviour could be observed throughout the night (Rufaut 1995). The wētā from rat-infested places (both mainland and islands) showed a significant increase in their occupancy of refuges, with a corresponding reduction in the duration of their activity periods, compared with wētā from rat-free islands. The 'experienced' wētā seemed to have a heightened awareness of movements and danger outside the refuge, in comparison with wētā from mammal-free locations.

Although these experimental examples show that 'predator experience counts', they do not indicate behavioural attributes of the large, avian-adapted invertebrates that were exterminated when rodents invaded New Zealand. They do, however, give a glimpse of the kind of behavioural adaptations that might have arisen under the selective influence of avian predators and today allow some species of large, flightless, nocturnal invertebrates to survive despite the presence of mammals.

(6) Taxonomic representation

New Zealand's fauna is notable for its missing groups (snakes, tortoises, scorpions), as well as for its specialised family-level endemics (Gibbs 2006). Can we find any invertebrate taxa whose presence or unusual characteristics could be cited as an example of the avian-driven history? Or are they simply quirks of biogeography?

Family-level endemics amongst the invertebrate groups are rare and in general include small and obscure forms that have no bearing on the issue of a bird-dominated history. In the insects, for example, the marine caddis family Chathamidae is unique for its departure from purely fresh water habitats, but not significant in terms of the avifauna. Interestingly, two insect groups represented in New Zealand are dependent on mammals, one more so than the other. The endemic butterfly family, *Mystacinobiidae*, which contains a single, unique, commensal fly species (*Mystacinobia zelandica*), unrelated to the butterflies of the rest of the world, has presumably evolved in New Zealand, adapted to the short-tailed bat (Gleeson et al. 2000). Then again, the true dung beetles (*Scarabaeinae*), which are generally diverse in mammal-dominated faunas, are represented in avian New Zealand by only two genera (*Saphobiomorpha* and *Saphobius*) in the primitive Gondwanan tribe Canthonini. Neither genus has species with a confirmed association with any form of dung. Apparently, the former is found in seabird carrion. Although readily attracted in large numbers to mammalian dung, *Saphobius* is common in leaf litter. Its normal food remains unknown. Perhaps more directly related to the absence of a mammalian fauna, New Zealand lacks the dominant world genus of advanced, true dung beetles, *Onthophagus*, very strong fliers with about 200 species in Australia and 2000 species world-wide (G. Monteith, Queensland Museum, pers. comm).

Another notable taxonomic shortcoming of New Zealand invertebrates is the extraordinarily depauperate fauna of ants and termites here, compared with Australia, the potential source area. Australia supports probably the richest and most diverse ant and termite fauna in the world, despite the presence of specialised ant-eating mammals. In New Zealand, it is likely the ant fauna has suffered serious depletion, probably as a

result of Pleistocene cold periods, but certainly not due to any bird dominance. It has been suggested the lack of a major ant presence in the litter has contributed to the richness of this zone for snails and small arthropods (GW Ramsay, unpubl. ms.).

So, the conclusion seems to be that the bird-driven environment of prehistoric New Zealand has left a few oversize, flightless insects, and possibly a fauna more cryptic than most. There are no distinctive morphological trademarks that reveal bird dominance in the invertebrate fauna. What is significant to an invertebrate, is the mortality inflicted by predation and their response to that mortality factor. Thus, to fully assess the result of an almost purely avian history, we must tackle the more difficult issue of predator avoidance behaviour: What behavioural attributes can we identify that secured an invertebrate species' survival with a bird-dominated predator fauna, but failed when modern rodents arrived?

The impact of introduced rodents on the New Zealand invertebrate fauna

The 80-million-year 'mammal-free experiment' (Gibbs, 2009; almost mammal-free, see Worthy et al. 2006) came to an abrupt end with the arrival of Polynesians in the 13th Century. For the next 500 years, kiore (*Rattus exulans*) shared the New Zealand environment with terrestrial microbats (microchiropteran bats), as the only mammalian predators of insects and other invertebrates (Holdaway 1999). The rat was mainly, but not entirely, confined to the main islands, leaving many smaller offshore islands as controls for the mammal-free experiment.

With the highly skilled, endemic avian predators, life for invertebrates was never secure, but with the advent of kiore the dangers escalated. Although our knowledge of the Quaternary insect fauna is very sketchy in comparison with that of the vertebrate fauna, it is sufficient to imply that this single rodent species selectively destroyed a number of large-bodied beetles prior to the arrival of Europeans with their associated mammals and insectivorous birds (Ramsay 1978a; Campbell et al. 1984). For many years, the evidence rested on the observation that many of the larger invertebrates have relict distributions on small islands and are absent or rare on the mainland (Worthy & Holdaway 2002). Today, Quaternary fossil material is known from four types of sites: feeding deposits of avian predators, caves and sinkholes, buried forests that have succumbed to volcanic ash showers, and Pleistocene deposits (where beetle remains have been recovered).

Two avian predators, laughing owl, now extinct, and New Zealand falcon (*Falco novaeseelandiae*), have obligingly left their nest debris on overhanging rocky outcrops, preserved for hundreds of years. These deposits, from 12 sites in Canterbury, South Island, have yielded over 40 beetle taxa (Kuschel & Worthy 1996). This collection contains, for example, two species of large flightless beetles, *Anagotis stephenensis* and *Amychus granulatus*, which are no longer known from the Canterbury regions where the raptors hunted, but still occur offshore, only on rat-free islands of the South Island (Kuschel & Worthy 1996).

From another source of beetle fossil material comes evidence of the extinction of two North Island species of large, flightless, forest beetle, some time between the Taupo eruption, 1800 yr BP, and the arrival of European naturalists. The fossils have been found in a limestone sinkhole at Waitomo and from under the ash layer in a buried podocarp forest deposit at Pureora (Kuschel 1987). One was the weevil *Tymbopiptus valeas* (23 mm in length), the other a large

Ulodidae, *Waitomophylax worthyi* (25 mm) (see Leschen & Rhode 2004 for nomenclature), from the same sinkhole at Waitomo and dated at 1680–2024 yr BP (Leschen & Rhode 2002). These authors, when discussing causes of extinction, suggest that, of all possible factors, introduced rodents are the most likely.

The common factors in these few recorded instances of invertebrate extinction on the New Zealand mainland were rodent invasion, large body size, flightlessness and a ground-active lifestyle, probably nocturnal. We can only speculate that perhaps the predominantly avian predator history in the evolution of these beetles rendered them more susceptible than they might otherwise have been. However, it must be admitted that we really have barely scratched the surface when it comes to the consideration of invertebrate extinctions in New Zealand. More will undoubtedly be documented as fossil material is catalogued, but by far the majority of Quaternary beetle specimens recovered so far are smaller than the above examples and can be identified as extant species (Marra 2008).

Conclusions

If we accept that moa herbivory, in lieu of mammal herbivory, has left an evolutionary footprint on the New Zealand flora, then what can be said about an avian-driven history and impact on the invertebrate fauna? Birds of all sizes, together with microbats, are the dominant vertebrate insectivores in all the world's biotas. A key question for New Zealand is whether the distinctive ground-active insectivorous bird guild, identified by Atkinson and Millener (1991), was unique enough to exert a measurable impact equivalent to moa herbivory? It must be admitted that the moa guild was exceptional; perhaps the guild of New Zealand's insectivorous birds was relatively ordinary by comparison. Also, perhaps the overall impact of the avian predators was tempered by the presence of kiwi, an unusual mammal-like bird, which, by all accounts, should have prepared the fauna exceptionally well for the subsequent mammal invasion.

I believe that ultimately it will be the non-morphological markers like odours, avoidance behaviours or activity patterns that will determine whether a bird or a mammal signature remains on the New Zealand invertebrate fauna.

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