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Diet, predators, and defensive behaviors of New Zealand harvestmen (Opiliones: Neopilionidae)

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Abstract. The Neopilionidae is a highly diversified harvestman family in New Zealand, comprising eight genera and 28 species. Although individuals of many species are abundant in the field, basic information on their natural history is absent. Here we describe the diet, predators, and defensive behaviors of 13 species across three genera, *Forsteropsalis* Taylor, 2013*, Mangatangi* Taylor, 2013*,* and *Pantopsalis* Simon, 1879. Using three years of field observations, we first identify food items for this family, finding that New Zealand neopilionids are opportunistic, generalist foragers with a diet composed of a wide variety of prey and scavenged soft-bodied invertebrates, including worms, amphipods, species from nine orders of insects, and two orders of arachnids (including conspecifics). We then describe the first known invertebrate predators of New Zealand harvestmen, including seven spider species, and conduct a review of the literature to collate a list of 32 species of native and non-native vertebrates (frogs, lizards, fish, birds, and mammals) that prey on harvestmen, including neopilionids. Finally, we describe the defensive behaviors of neopilionids, providing the first reports of autotomy and thanatosis in the family. In general, the diet of New Zealand neopilionids is similar to other harvestman species, and the list of predators includes mostly insectivorous taxa known to feed on harvestmen elsewhere. The defensive repertoire of neopilionids includes behaviors recorded for other species of Eupnoi, such as leg autotomy, but also unique behaviors that are only known for species of Dyspnoi and Laniatores, such as thanatosis.

Keywords: Prey, natural enemies, predation, cannibalism, autotomy

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Harvestmen are a highly diversified group of arachnids, comprising nearly 6,500 species worldwide, with great variation in their morphology, ecology, and behavior (Machado et al. 2007). Unlike most arachnids, which are mainly predators, harvestmen are typically omnivorous with the ability to masticate and ingest solid food (reviewed in Acosta & Machado 2007). Some species are known to be competent predators (e.g., Castanho & Rocha 2005; Benson & Chartier 2010; Wolff et al. 2016), while also heavily relying on opportunistic scavenging of animal remains (e.g., Sankey 1949; Gnaspini 1996; Morse 2001). Plant materials, such as fruits and inflorescences, are also consumed, though animal matter is usually preferred (Gnaspini 1996; Halaj & Cady 2000; Machado & Pizo 2000; but see Schaus et al. 2013). A few examples of dietary specialists are found among the order, most notably the family Trogulidae that specifically eat live snails and then utilize the remaining shell for oviposition (Pabst 1953; Martens 1978; Komposch 1992). However, most species of harvestmen for which the diet is known are generalists that accept a wide range of food items, primarily invertebrates (reviewed in Acosta & Machado 2007).

To date, the foraging behavior of only a few species of New Zealand harvestmen has been documented. In his monograph on New Zealand harvestmen of the family Triaenonychidae, Forster (1954) reported that the food items consumed by the species "consist mainly of insects and other small arthropods". He never observed the capture of live prey, and under laboratory conditions the individuals fed only on dead insects. A more detailed account on the diet of a New Zealand harvestman was provided for *Forsteropsalis photophaga* Taylor & Probert, 2014 (previously misidentified as *Megalopsalis tumida* (Forster, 1944) (see Taylor & Probert 2014)), a representative of the family Neopilionidae that preys upon the larvae, pupae, and winged adults of the endemic glow-worm *Arachnocampa luminosa* (Diptera: Keroplatidae) in the cave systems in which they live (Richards 1960; Meyer-Rochow & Liddle 1988; Broadley 2012). With an interest in the ecophysiology of cave-dwelling predators exposed to bioluminescent light sources in these otherwise dark cave systems, Meyer-Rochow & Liddle (1988) investigated the vision of *F. photophaga* and another cave-dwelling harvestman, the triaenonychid *Hendea myersi* Forster, 1954. The authors showed that individuals of *F. photophaga* find the glow-worms using the light they emit, which constitutes the only formal record of a harvestman using visual cues to find prey (Meyer-Rochow & Liddle 1988). However, it is unclear whether *F. photophaga* solely specializes on *A. luminosa* or whether other food items are accepted.

Like many other arachnids, harvestmen are also prey for other species, including both invertebrates and vertebrates. An extensive review of their natural enemies demonstrated that harvestmen are consumed by a wide range of generalist predators, such as flatworms, spiders, scorpions, centipedes, ants, ground beetles, assassin bugs, amphibians, reptiles, mammals, and birds (Cokendolpher & Mitov 2007). However, no predators listed in this review were known from New Zealand studies. The review on harvestman predators mentions that hedgehogs (*Erinaceus europaeus*) include harvestmen in their diet in Europe (Sankey 1949), but no studies from New Zealand were cited, even though this mammal species was introduced in the country in the late 19th century and is now well established (Brockie 1990). European birds, such as the dunnock (*Prunella modularis*), starling (*Sturnus vulgaris*), and rook (*Corvus frugilegus*), which were also introduced in New Zealand, are known to feed on harvestmen (see references in Cokendolpher & Mitov 2007), but all studies included in the review were conducted in their native range (Tomek 1988; Cramp & Perrins 1994). Thus, despite no representation of predation on New Zealand harvestmen specifically mentioned in the review by Cokendolpher & Mitov (2007), we expect that many invasive, and perhaps some native species known to be insectivorous, would also predate upon harvestmen.

To cope with a wide variety of predators, harvestmen exhibit highly diverse defensive strategies that include both primary defenses, such as camouflage, aposematism, and aggregations, and secondary defenses, such as thanatosis, leg autotomy, chemical defense, and "bobbing" (reviewed in Gnaspini & Hara 2007). Some of these defensive strategies, such as camouflage, aggregations, thanatosis, and chemical defense are widespread in the order, with records in the suborders Eupnoi, Dyspnoi, and Laniatores, which are the most intensively studied suborders of Opiliones (see examples in Gnaspini & Hara 2007). In turn, other defensive strategies, such as leg autotomy and bobbing, are restricted to certain clades of the suborder Eupnoi, which includes many of the long-legged harvestmen (see examples in Gnaspini & Hara 2007). Although it should be expected that at least leg autotomy would be present in species of the family Neopilionidae (Eupnoi), there is no formal record of this behavior reported for a New Zealand species. Indeed, like most aspects of the natural history and ecology of harvestmen in the country, the defensive strategies have not been formally described for any native species of the order Opiliones.

Here we provide the first detailed account of the natural history of several species of New Zealand Neopilionidae, a family with great diversity in the country. First, we describe a list of food items consumed by neopilionids and provide a few accounts of notable behaviors associated with foraging, such as scavenging and predation behaviors, conspecific and heterospecific competition, food sharing, and cannibalism. Second, we present direct observations of predation events in the field to produce a list of invertebrate predators of neopilionids. We also conducted a literature review of diet records for New Zealand taxa and collated a list of species for which harvestmen were known prey (32 species across reptiles, amphibians, fish, birds, and mammals). Finally, we describe the defensive behaviors utilized by the neopilionids, with emphasis on leg autotomy.

METHODS

Study species and localities.—Our field observations on the food items, predators, and defensive behaviors were focused on 13 species of the family Neopilionidae from New Zealand: *Forsteropsalis bona* Taylor & Probert, 2014, *F. chiltoni* (Hogg, 1910), *F. fabulosa* (Phillipps & Grimmett, 1932), *F. inconstans* (Forster, 1944), *F. marplesi* (Forster, 1944), *F. photophaga*, *F. pureora* Taylor, 2013, *F. wattsi* (Hogg, 1920), *Mangatangi parvum* Taylor, 2013, *Pantopsalis albipalpis* Pocock, 1902, *P. coronata* Pocock, 1903, *P. listeri* (White, 1849), and *P. phocator* Taylor, 2004. With the exception of *F. photophaga*, which is a cave dweller only encountered in this habitat, and *F. bona*, which is frequently found deep inside caves but may also venture out to associated rock walls and stream banks, all other species are forest dwellers that are found mainly on the low vegetation, tree trunks, and boulders, and are often associated with freshwater aquatic environments, such as streams, waterfalls, gorges, and dams. Field observations were concentrated at night (between 2200 h and 0400 h), when individuals are more active. Some species (e.g., *F. bona, F. pureora*, and *P. listeri*) were maintained in captivity for behavioral observations, and we presented them with several food items. All food items accepted by captive individuals were included in the list provided in Table 1.

The following localities were visited for data collection: Hakarimata Ranges (37°39′47.5″S 175°08′14.6″E), Ngaruawahia, North Island; Ruakuri Bushwalk (38°15′53.7″S 175°04′46.4″E), Waitomo, North Island; private land (38°15′41.4″S 175°00′53.6″E), Waitomo, North Island; Tawarau Forest (38°17′24.8″S 174°56′50.2″E), Te Anga, North Island; Marokopa Falls Track (38°15′33.6″S 174°50′54.6″E), Te Anga, North Island; Mangapohue Natural Bridge (38°15′39.6″S 174°53′56.4″E), Te Anga, North Island; Tauranga Bridge (38°12′16.2″S, 177°17′46.6″E), Waioeka Gorge, North Island; Belmont Regional Park (41°09′25.7″S 174°57′57.6″E), Upper Hutt, North Island; Golden Fleece Battery Walk (42°07′48.7″S 171°52′57.8″E), Victoria Forest, South Island; Emily Falls Track (43°53′45.6″S 171°13′40.8″E), Peel Forest, North Island; Sullivan's Dam (45°48′19.4″S 170°31′10.2″E), Leith Valley Road, Dunedin, South Island; McLean Falls (46°34′23.7″S 169°20′47.7″E), Catlins Forest Park, Owaka, South Island; Raroa Track (46°54′01.7″S 168°07′20.1″E), Oban, Stewart Island; Fuschia Track (46°54′00.1″S 168°07′30.0″E), Oban, Stewart Island; and Track at Peterson Hill Road and Deep Bay (46°54′12.7″S 168°08′08.6″E), Oban, Stewart Island. This list represents the coordinates of sites visited by the authors for observations presented herein, but does not capture localities included in personal communications, iNaturalist (inaturalist.org) observations, or the published literature on harvestman predators from our literature review. The locations for these other records are listed in Tables 1 and 2.

Diet.—We describe the diet of New Zealand harvestman species based on direct observations. To add to this dataset, we then sourced research-grade photographs from iNaturalist, where locality and dates were provided, and photos were clear enough to identify harvestmen to genus or species level and prey items to at least order level. A food item was considered scavenged if it appeared dried (often broken into several pieces), otherwise deteriorated, or if it had apparently begun to decompose (following Machado et al. 2000). Where prey capture was observed and where prey was still moving or if the location where the harvestmen opened the integument was clearly fresh tissue, we determined that live prey had most likely been caught alive by the harvestman (following Machado et al. 2000). If we were still not sure if the food item was scavenged or captured, we attempted to contact the photographers of iNaturalist photos for more information about the observation. In the cases where it was impossible to determine, we note that it is unknown whether food items were scavenged or predated.

We also conducted a literature search to find any documented food items of Neopilionidae by performing Google Scholar record searches for any records pertaining to

Table 1.—A complete list of identified food items of several species of New Zealand Neopilionidae.

Species	Sex (maturity)	Prey item	Prey status	Location	Source
Forsteropsalis bona	Male (adult)	Conspecifics (adult males and juvenile)	Captured	In captivity (collected in Waitomo)	E.C. Powell pers. obs.
	Male (adult)	Diptera: Calliphoridae	Scavenged	Waitata, Bay of Plenty	C.J. Painting pers. obs. (Fig. 1f)
	Female (adult)	Orthoptera: Anostostomatidae	Captured	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs. (Fig. 1d)
	Males & females (juveniles & adults)	Wet dog food, carrot, and apple	Not applicable	In captivity (collected in Waitomo)	E.C. Powell pers. obs.
Forsteropsalis chiltoni	Male (adult)	*Leptotarsus* sp. (Diptera: Tipulidae)	Captured	Oban, Stewart Island	E.C. Powell pers. obs. (Fig. 1b)
Forsteropsalis fabulosa	Female (adult)	Ephemeroptera	Captured	Upper Hutt, Wellington	E.C. Powell pers. obs.
Forsteropsalis inconstans	Male (adult)	*Cycloctenus* sp. (Araneae: Cycloctenidae)	Scavenged	Wainuiomata, Lower Hutt	iNaturalist (U. Schneehagen) (Fig. 3c)
	Male (subadult)	Amphipoda	Scavenged	Wainuiomata, Lower Hutt	iNaturalist (U. Schneehagen) (Fig. 5)
	Male (subadult)	*Schedotrigona* sp. (Diplopoda: Schedotrigonidae)	Captured	Korokoro, Lower Hutt	iNaturalist (U. Schneehagen) (Fig. 1a)
	Male (adult)	Ephemeroptera	Captured	Wainuiomata, Lower Hutt	iNaturalist (U. Schneehagen) (Fig. 1c)
	Female (adult)	Orthoptera	Captured	Brooklyn, Wellington	iNaturalist (W. Brockelsby)
	Unknown sex (juvenile)	*Hemideina* sp. leg only (Orthoptera: Anostostomatidae)	Scavenged	Brooklyn, Wellington	iNaturalist (W. Brockelsby)
	Male (adult)	*Halmus chalybeus* (Coleoptera: Coccinellidae)	Captured	Waiwhetu, Lower Hutt	iNaturalist (U. Schneehagen) (Fig. 1h)
	Female (adult)	Coleoptera: Scarabaeidae, Melolonthinae	Scavenged	Rimutaka Hill, Tauherenikau	iNaturalist (L. Bennett)
	Female or juvenile	*Apis mellifera* (Hymenoptera: Apidae)	Unknown	Karori, Wellington	iNaturalist (A. Simpson)
	Male (subadult)	Diptera	Scavenged	Wellington	iNaturalist (D. Townsend)
Forsteropsalis marplesi	Female (adult)	*Apis mellifera* (Hymenoptera: Apidae)	Captured	Sullivan's Dam, Dunedin	E.C. Powell pers. obs.
Forsteropsalis photophaga	Males & females (adult)	*Arachnocampa luminosa* (Diptera: Keroplatidae): larvae, pupae & adults	Captured	Waitomo Caves	Richards (1960); Pugsley (1984); Meyer-Rochow & Liddle (1988); Broadley (2012) under the misidentified name *Megalopsalis tumida*
Forsteropsalis pureora	Unknown sex (juvenile)	*Cambridgea* sp. (Araneae: Desidae)	Scavenged	Te Anga	E.C. Powell pers. obs. (Fig. 3a)
	Female (adult)	*Cycloctenus* sp. (Araneae: Cycloctenidae)	Scavenged	Te Anga	E.C. Powell pers. obs. (Fig. 3b)
	Female (adult)	Droppings from the web of *Leucauge dromederia* (Araneae: Tetragnathidae)	Scavenged	Ruakuri Natural Bridge, Waitomo	E.C. Powell & M. Merien pers. obs.
	Male (adult)	Amphipoda	Unknown	Mangapohue Natural Bridge, Te Anga	E. C. Powell pers. obs. (Fig. 2e)
	Male (adult)	Odonata (Anisoptera)	Scavenged	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs. (Fig. 2d)
	Female (adult)	Orthoptera: Rhaphidophoridae	Scavenged	Hakarimata Ranges, Ngaruawahia	E.C. Powell pers. obs.

Table 1.—Continued.

Species	Sex (maturity)	Prey item	Prey status	Location	Source
	Female (adult)	Phasmida	Scavenged	Hakarimata Ranges, Ngaruawahia	E. C. Powell pers. obs.
	Male (adult)	*Celatoblatta* sp. (Blattodea: Blattidae)	Scavenged	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs. (Fig. 2c)
	Male (adult)	Hemiptera: Pentatomomorpha	Unknown	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs.
	Male (adult)	*Scolypopa australis* (Hemiptera: Ricaniidae)	Scavenged (wrapped in silk)	Hamilton	B. McQuillan pers. comm.
	Male (adult)	Coleoptera: Scarabaeidae, Melolonthinae	Scavenged	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs. (Fig. 2b)
	Male (adult)	*Vespula* sp. (Hymenoptera: Vespidae)	Unknown	Ruakuri Natural Bridge, Waitomo	E.C. Powell pers. obs.
	Male (adult)	Lepidoptera (larva)	Captured	Te Anga	E.C. Powell pers. obs. (Fig. 2a)
	Male (subadult)	Lepidoptera: Tortricidae (adult)	Captured	Te Anga	E.C. Powell pers. obs. (Fig. 1e)
	Male (adult)	Diptera: Muscidae (adult)	Captured	In captivity (collected in Waitomo)	E.C. Powell pers. obs.
	Males & females (juveniles & adults)	Wet dog food, carrot, lettuce, apple, and mango	Not applicable	In captivity (collected in Waitomo)	E.C. Powell pers. obs.
Forsteropsalis wattsi	Male (adult)	Annelida	Captured	Marlborough Sounds	D. Hegg pers. comm.
Mangatangi sp.	Male (adult)	Hymenoptera: Megachilidae	Scavenged	Wilton, Wellington	iNaturalist (W. Brocklesby)
	Unknown	Lepidoptera (larva)	Scavenged	Karori, Wellington	iNaturalist (T. Wills)
Pantopsalis listeri	Male (adult)	Hemiptera: Pentatomidae	Unknown	Te Anga	E.C. Powell pers. obs.
	Male and female (adults)	Diptera: Calliphoridae	Scavenged	Hari Hari, West Coast	S. Pollard pers. comm. (Fig. 4)
	Males & females (juveniles & adults)	Wet dog food, carrot, and apple	Not applicable	In captivity (collected in Waitomo and Te Anga)	E.C. Powell & C.J. Painting pers. obs.
Pantopsalis phocator	Male (adult)	Opiliones: Neopilionidae (juvenile)	Captured	Sullivan's Dam, Dunedin	E.C. Powell pers. obs.
	Male (adult)	Diptera (adult)	Scavenged	Oban, Stewart Island	E.C. Powell pers. obs. (Fig. 1g)
Pantopsalis sp.	Females	Oligochaeta	Scavenged	Paparoa National Park	iNaturalist (Aeterno)
	Female (adult)	*Nuncia* sp. (Opiliones: Triaenonychidae)	Scavenged	Haast, Westland	J. Warfel pers. comm. (Fig. 3d)
	Female (adult)	Lepidoptera: Geometridae (larva)	Captured	Papatowai	iNaturalist (D. Holland)
Megalopsalis sp.*	Unspecified	Carrot and pollard baits (with and without sodium monofluoroacetate "1080")	Not applicable	Ohakune	Sherley et al. (1999)
Opiliones (unspecified)	Unspecified	Decomposing squid bait	Not applicable	Aorangi and Remutaka Forests	Vergara Parra (2018)

* All but one species in the genus *Megalopsalis* in New Zealand have now been transferred to the genus *Forsteropsalis* (Taylor 2011).

Table 2.—List of the known predators of Opiliones in mainland New Zealand and offshore islands. This list combines new observations of predators and a review of diet records in the literature. Method: DO = direct observation, SC = stomach contents, GC = Gizzard contents, FS = fecal samples, RP = regurgitated pellets.

Predator	Opiliones prey	Location	Method	Source
Invertebrate:				
Australomimetus sennio (Araneae: Mimetidae)	*Forsteropsalis pureora* (adult female)	Rotorua, North Island	DO	B. McQuillan pers. comm.
Cambridgea sp. (Araneae: Desidae)	*Forsteropsalis pureora* (adult male)	Waitomo, North Island	DO	E.C. Powell pers. obs. (Fig. 7d) G.I. Holwell pers. obs.
Dolomedes minor (Araneae: Pisauridae)	*Forsteropsalis pureora* (adult male)	Hamilton, North Island	DO	B. McQuillan pers. comm.
Taraire rufolineata (Araneae: Tetragnathidae)	*Forsteropsalis inconstans* (adult male)	Kahurangi National Park, Tasman, South Island	DO	D. Hegg pers. comm.
Sidymella angularis (Araneae: Thomisidae): female	*Forsteropsalis chiltoni* (juvenile)	Oban, Stewart Island	DO	E.C. Powell pers. obs. (Fig. 7a)
Theridion zanthalabio (Araneae: Theridiidae): female	*Forsteropsalis inconstans* (adult male)	Muritai, Lower Hutt, North Island	DO	U. Schneehagen pers. comm. (Fig. 7b)
Uliodon sp. (Araneae: Zoropsidae) adult male	*Forsteropsalis pureora* (adult male)	Waitomo, North Island	DO	E.C. Powell pers. obs.
Uliodon sp. (Araneae: Zoropsidae) adult female	*Forsteropsalis pureora* (adult male)	Ngaruawahia, North Island	DO	E.C. Powell pers. obs. (Fig. 7c)
Unknown araneoid spider (Araneae)	*Forsteropsalis pureora* (adult male)	Waitomo, North Island	DO	E.C. Powell pers. obs.
Unknown araneoid spider (Araneae)	*Pantopsalis phocator* (adult male)	Waitomo, North Island	DO	E.C. Powell pers. obs.
Forsteropsalis bona (Opiliones: Neopilionidae): adult male	Conspecific juveniles and adult males	In captivity (collected in Waitomo, North Island)	DO	E.C. Powell pers. obs.
Pantopsalis phocator (Opiliones: Neopilionidae): adult male	Juvenile Neopilionidae (unidentifiable)	Catlins Forest Park, Southland, South Island	DO	E.C. Powell pers. obs.
Vertebrate:				
Leiopelma hochstetteri & *L. archeyi* (Amphibia, Anura: Leiopelmatidae)	Opiliones (unspecified)	Coromandel Peninsula & Pureora Forest, North Island	SC	Shaw et al. (2012)
Sphenodon punctatus (Reptilia, Rhynchocephalia: Sphenodontidae)	Opiliones (unspecified)	Stephens Island, Cook Strait	FA	Walls (1981)
Sphenodon punctatus (Reptilia, Rhynchocephalia: Sphenodontidae)	Opiliones (unspecified)	Lady Alice Island	SC	Ussher (1999)
Leiolopisma inconspicuum, L. maccanni & *L. nigriplantare polychrome* (Reptilia, Squamata: Scincidae)	Opiliones (unspecified)	Central Otago, South Island	SC	Patterson (1992)
Leiolopisma zealandicum & *Leiolopisma* sp. (Reptilia, Squamata: Scincidae)	Opiliones (unspecified)	Manawatu, North Island	SC	Gill (1976)
Oligosoma smithi (Reptilia, Squamata: Scincidae)	Opiliones (unspecified)	Tawharanui, Regional Park, North Island	DO*	Wedding et al. (2010)
Galaxias brevipinnis (Actinopterygii, Galaxiiformes: Galaxiidae)	Opiliones (unspecified)	South Westland, South Island	SC	Main & Winterbourn (1987)
Anas chlorotis (Aves, Anseriformes: Anatidae)	Opiliones (unspecified)	Great Barrier Island	SC & FS	Moore et al. (2006)
Apteryx mantelli (Aves, Apterygiformes: Apterygidae)	Opiliones (unspecified)	Waihi, North Island	SC	Gurr (1952)
Urodynamis taitensis (Aves, Cuculidae: Cuculiformes)	Opiliones (unspecified)	Auckland, North Island	GC	Gill (1980)
Corvus frugilegus (Aves, Passeriformes: Corvidae)	Opiliones (unspecified)	Hawkes Bay, North Island	GC	Porter (1979)
Gerygone igata (Aves, Passeriformes: Acanthizidae)	Opiliones (unspecified)	Orongorongo Valley, Wellington, North Island	FS	Moeed & Fitzgerald (1982)
Gymnorhina tibicen (Aves, Passeriformes: Artamidae)	*Phalangium opilio*	Christchurch airport, South Island	GC	Moeed (1976)
Megalurus punctatus (Aves, Passeriformes Locustellidae): nestlings	Opiliones (unspecified)	Invercargill, South Island	GC	Barlow & Moeed (1980)

Table 2.—Continued.

Predator	Opiliones prey	Location	Method	Source
Petroica macrocephala toitoi (Aves, Passeriformes: Petroicidae)	Opiliones (unspecified)	Orongorongo Valley, Wellington, North Island	FS	Moeed & Fitzgerald (1982)
Prunella modularis (Aves, Passeriformes: Prunellidae)	Opiliones (unspecified)	Orongorongo Valley, Wellington, North Island	FS	Moeed & Fitzgerald (1982)
Rhipidura fuliginosa (Aves, Passeriformes: Rhipiduridae)	Opiliones (unspecified)	Orongorongo Valley, Wellington, North Island	FS	Moeed & Fitzgerald (1982)
Sturnus vulgaris (Aves, Passeriformes: Sturnidae): adults	*Phalangium opilio*	Christchurch airport, South Island	GC	Moeed (1976)
Sturnus vulgaris (Aves, Passeriformes: Sturnidae): nestlings	*Phalangium opilio*	Hawkes Bay, North Island	GC	Moeed (1980)
Zosterops lateralis (Aves, Passeriformes: Zosteropidae)	Opiliones (Phalangiidae)	Nelson, South Island	SC	Moeed (1979)
Athene noctua (Aves, Strigiformes: Strigidae)	Opiliones (unspecified)	Birds included from across NZ	SC	Marples (1942)
Ninox novaeseelandiae (Aves, Strigiformes: Strigidae)	Opiliones (Phalangida)	Pureora Forest, North Island	RP	Haw & Clout (1999); Haw et al. (2001)
Mustela erminea (Mammalia, Carnivora: Mustelidae)	Opiliones (unspecified)	South Westland, South Island	SC	Rickard (1996)
Mystacina tuberculata (Mammalia, Chiroptera: Mystacinidae)	Opiliones (unspecified)	Little Barrier Island	FS	Arkins et al. (1999)
Trichosurus vulpecula (Mammalia, Diprotodontia: Phalangeridae)	Opiliones (unspecified)	Orongorongo Valley, Wellington, North Island	SC	Cowan & Moeed (1987)
Erinaceus europaeus (Mammalia, Eulipotyphla: Erinaceidae)	*Phalangium opilio*	Canterbury, South Island	SC & FS	Campbell (1973)
Erinaceus europaeus (Mammalia, Eulipotyphla: Erinaceidae)	Opiliones (unspecified)	Auckland, North Island	SC	Jeffries (2011)
Erinaceus europaeus (Mammalia, Eulipotyphla: Erinaceidae)	Opiliones (unspecified)	Auckland, North Island	SC	Nottingham et al. (2019)
Rattus exulans (Mammalia, Rodentia: Muridae)	Opiliones (unspecified)	Rakiura, Stewart Island	SC	Sturmer (1988)
Rattus norvegicus (Mammalia, Rodentia: Muridae)	Opiliones (unspecified)	Kapiti Island	SC	Dick (1985)
Rattus norvegicus (Mammalia, Rodentia: Muridae)	Opiliones (unspecified)	Rakiura, Stewart Island	SC	Sturmer (1988)
Rattus rattus (Mammalia, Rodentia: Muridae)	Opiliones (unspecified)	Rakirua, Stewart Island	SC	Sturmer (1988)
Rattus rattus (Mammalia, Rodentia: Muridae)	Opiliones (one Eupnoi noted)	Fiordland National Park, South Island	SC	Clapperton et al. (2019)
Rattus rattus (Mammalia, Rodentia: Muridae)	Opiliones (long-legged specified)	South Westland, South Island	SC	Rickard (1996)

* Skinks ate harvestmen in pitfall traps associated with bait station study.

the taxa: "Neopilionidae", "Monoscutidae" (former family name), "*Acihasta*", "*Americovibone*", "*Forsteropsalis*", "*Mangatangi*", "*Megalopsalis*", "*Monoscutum*", "*Pantopsalis*", and "*Templar*". We also conducted more generic searches for "New Zealand" paired with "Opiliones", "harvestmen", "harvestman", or "daddy long legs" in case harvestmen were mentioned but not identified to the family level.

Predators.—We collected information on the predators of the New Zealand Neopilionidae via direct observations in the field and by reviewing prey records across the literature for species known to forage on invertebrates. We found that prey types for invertebrate predators in New Zealand are largely undocumented. For vertebrate species (which usually relied on gut content or fecal analysis), dietary records were far more abundant in number, yet these studies rarely identified the harvestmen prey past the order level. In fact, many studies we found during our review did not classify prey types past class Arachnida and these studies were not included here. Thus, it was possible that Opiliones prey listed in the literature could belong to any of the following taxa present in New Zealand: (1) the introduced European harvestman *Phalangium opilio* Linnaeus, 1758 (Eupnoi, Phalangiidae), which has occurred in New Zealand since at least 1947 (Forster 1947); (2) endemic short-legged harvestmen in the family Triaenonychidae and Synthetonychiidae (Laniatores), with over 100 species recorded in the country (Forster 1954); (3) endemic species of mite harvestmen in the family Pettalidae (Cyphophthalmi), with over 30 species recorded in the country (Boyer & Giribet 2009); (4) the endemic *Acropsopilio neozelandiae* Forster, 1948 (Dyspnoi) (Forster 1948); and (5) our focal group, the long-legged Neopilionidae (Taylor 2004, 2011). In some cases, where predators were surveyed on farmland versus native forest, it is much more likely that the harvestmen predated were the non-native *P. opilio*, as this species is much more likely to occur in open habitats, including cleared pastureland, dirt tracks, and near urban dwellings (Edgar 1971; Curtis & Machado 2007). In contrast, endemic harvestmen are largely restricted to native forest (Forster 1954; Vélez et al. 2014). Despite our inability to determine the exact taxa of harvestmen for many published records, most vertebrate predators that live in disturbed habitats also thrive in native forest. If these species feed on *P. opilio*, they are also likely to feed on native species, such as neopilionids, which are similar in size and have similar defense strategies.

To thoroughly search for prey records of all potential predators in New Zealand, we used the key word "New Zealand" paired with generic terms "Opiliones", "harvestmen", "harvestman", or "daddy long legs", performing several Google Scholar searches which included harvestmen not identified past order-level. We also conducted literature searches for any records pertaining to the taxa: "Neopilionidae", "Monoscutidae", "*Acihasta*", "*Americovibone*", "*Forsteropsalis*", "*Mangatangi*", "*Megalopsalis*", "*Monoscutum*", "*Pantopsalis*", and "*Templar*". We then searched with key words "New Zealand" and "prey", paired with either "mammal", "reptile", "bird", "spider", "arachnid", or "invertebrate", and exhaustively searched text and tables for any papers about species expected to be insectivorous. From there, we inspected every source that met these criteria and back searched using the cited and citing references of those papers. Our aim was not to quantify the proportion of Opiliones that each predator species consumed in their overall diet, but to document any predators known to take harvestmen as prey. Methodology and sample sizes varied greatly between studies and prey records varied between localities when predator species were surveyed multiply. However, we do make note of the few taxa for which harvestmen made up a significant proportion (more than 10%) of the total prey in the study.

Defense.—During collections in the field, we recorded the defensive behaviors exhibited by the individuals of all neopilionid species we found. Given that the definition of some defensive behaviors varies in the literature, we characterize the most common defensive behaviors observed in the neopilionids as follows: (1) leg autotomy: is the act of self-amputating a limb (such as a leg) in response to a stimulus such as being grabbed by a predator (Fleming et al. 2007); (2) thanatosis (or tonic immobility): is the adoption of a motionless posture by a prey individual, triggered by physical contact or very close proximity of a predator (Humphreys & Ruxton 2018); (3) aggregation: in harvestmen, it is a group of three or more motionless individuals, with their bodies 0–5 cm apart from each other and legs overlapping (Machado et al. 2000); (4) bobbing: in harvestmen, it is a rapid up-and-down vibration of the body (Berland 1949); (5) fleeing: consists of a rapid movement away from the stimulus source, i.e., the predator (Edmunds 1974).

RESULTS

Diet.—We found that members of the genera *Forsteropsalis* Taylor, 2013*, Pantopsalis* Simon, 1879*,* and *Mangatangi* Taylor, 2013 are both opportunistic predators of live prey and readily scavenge on a wide range of invertebrates (Table 1; Figs. 1–3). Food items (both scavenged and captured) included earthworms, amphipods, insects such as bees, beetles, bugs, cockroaches, dragonflies, flies, mayflies, moths, and wētā, and arachnids such as spiders and harvestmen, including conspecifics (Table 1). Individuals of both sexes were able to capture and subdue live prey as large as themselves despite having no venom or silk (Fig. 1). It is important to note that our observations are likely biased towards larger food items, which are easier to identify, take longer to consume, and are thus more likely to be observed in the field. Multiple observations ($n = 17$) were made where harvestmen were clearly feeding on some animal matter, but the food item was too small to be identifiable.

In two instances, multiple individuals shared or competed over food items: (a) three females of *Pantopsalis* sp. were found sharing a large dead worm (Oligochaeta), and (b) a male *P. listeri* was observed using his chelicerae to tear open a scavenged calliphorid fly exposing the soft integument, and stepping back to allow a conspecific female to feed (S. Pollard pers. comm.) (Fig. 4). Harvestmen also seemingly competed with heterospecifics for scavenged prey. In one observation, a juvenile *F. inconstans* was witnessed struggling to keep scavenged amphipod prey from a millipede (Fig. 5). While it was unclear whether the harvestman or the millipede had the amphipod prey first, the juvenile *F. inconstans* was successful in keeping the amphipod from the millipede and carried it away (U. Schneehagen pers. comm.). This observation is

Figure 1.—New Zealand Neopilionidae with an assortment of freshly captured invertebrate prey. (a) Subadult male *Forsteropsalis inconstans* feeding on a millipede, *Schedotrigona* sp. (Diplopoda: Metopidiotrichidae), in Lower Hutt. (b) Adult male *F. chiltoni* feeding on a large crane fly (Diptera: Tipulidae) in Oban, Stewart Island. (c) Adult male *F. inconstans* feeding on a mayfly (Ephemeroptera) in Upper Hutt. (d) Adult female *F. bona* feeding on a small wētā (Orthoptera: Anostostomatidae) nymph in Waitomo. (e) Juvenile *F. pureora* feeding on a moth (Lepidoptera) in Waitomo. (f) Adult male *F. bona* feeding on a blow fly (Diptera: Calliphoridae) in Waitata, Bay of Plenty. (g) Adult male *Pantopsalis phocator* feeding on a fly (Diptera) in Dunedin. (h) Adult male *F. inconstans* feeding on a steelblue ladybird prey, *Halmus chalybeus* (Coleoptera: Coccinellidae), in Lower Hutt. Photographs (a), (c), (h) by U. Schneehagen, (f) by C. Painting, and (b), (d), (e), (g) by E.C. Powell.

interesting because millipedes rarely consume animal matter (Hopkin & Read 1992).

To capture live prey, individuals of all neopilionids studied here rest upon vegetation or rock walls at night and use a sit-and-wait hunting strategy, probably relying on movement and/or vibrations detected by the legs to recognize potential live prey. As invertebrates pass by, individuals first use their chelicerae to strike and subdue prey. Chelicerae are then aided by the pedipalps in manipulating the prey and bringing it to the mouthparts. Our observations of hunting by non-cavernicolous neopilionids mirrored the observations for *F. photophaga*, which also used their chelicerae to grab and

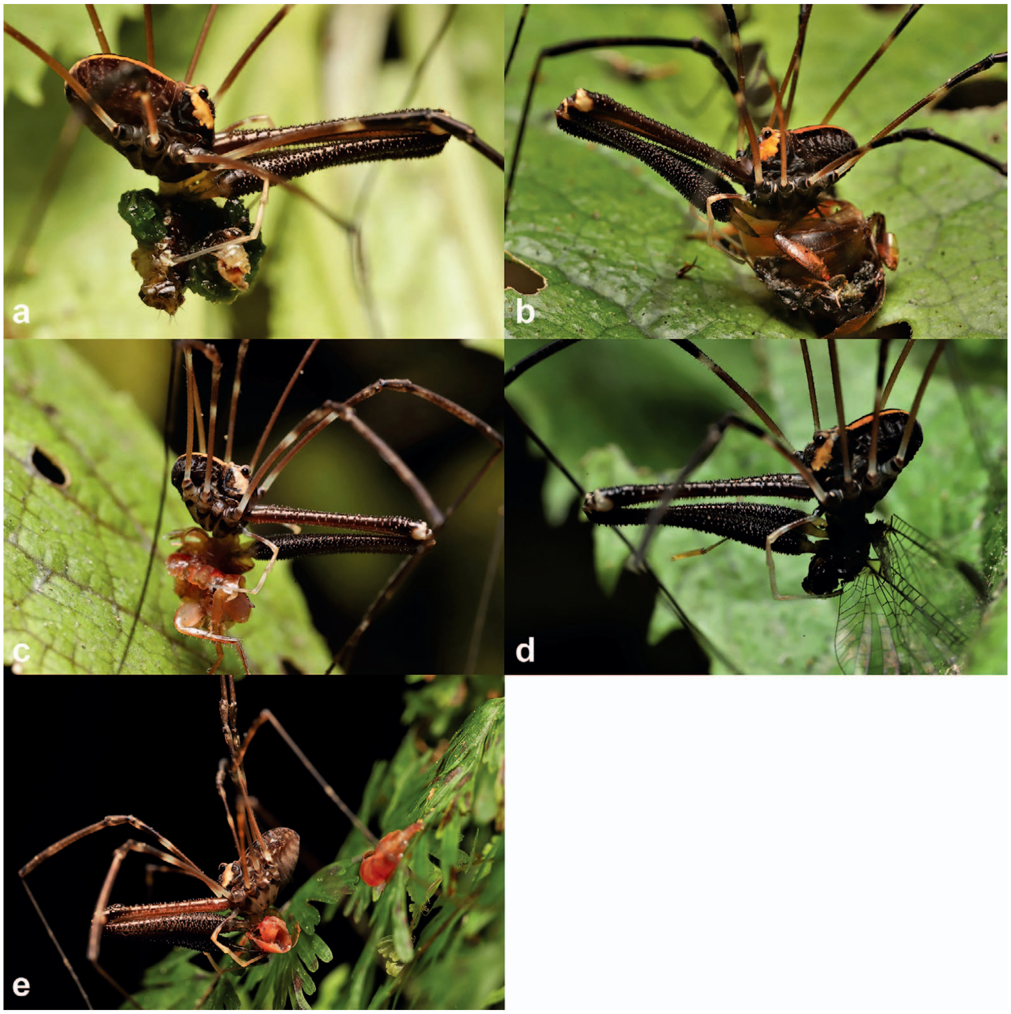

Figure 2.—Adult male *Forsteropsalis pureora* with captured and scavenged food items in Waitomo, New Zealand. (a) Adult feeding on a live-captured Lepidoptera larva. (b) Adult feeding on a scavenged chafer beetle (Coleoptera: Scarabaeidae). (c) Adult feeding on a scavenged cockroach (Blattodea) nymph. (d) Adult feeding on a scavenged dragonfly (Odonata). (e) Adult feeding on amphipod prey. All photographs by E.C. Powell.

subdue *Arachnocampa luminosa* prey (Richards 1960; Broadly 2012). Like some species of Australian Neopilionidae described in Wolff et al. (2016), some New Zealand species have plumose setae on the pedipalps. In adult male and female *F. photophaga*, the pedipalps are covered in plumose setae. No other species studied here have as apparent plumose setae in adult males. As plumose setae on the pedipalps are linked to adhesive properties used in hunting (Wolff et al. 2016), it is possible that the pedipalps of *F. photophaga* function specifically for hunting in the cave environment, perhaps to aid in capturing the *A. luminosa* they are known to prey upon.

There appear to be no marked differences between males and females in the type of diet or frequency of predation on live prey versus opportunistic scavenging (Table 1). One of the most impressive prey captures observed was by a female *F. marplesi* (with reduced chelicerae when compared with conspecific males) that captured a live honey bee (*Apis mellifera*) at night. Another interesting observation was an adult female *F. pureora* resting on the broad leaves of parataniwha (*Elatostema rugosum*) beneath the web of a long-jawed orb-weaver spider *Leucauge dromedaria* (Thorell, 1881) (Tetragnathidae). While the spider's prey was unidentifiable, we observed the female harvestman foraging on the parts of exoskeleton as it dropped onto the leaves beneath.

We also observed predation of harvestmen by harvestmen in natural field settings and also in captivity. First, an adult male of *P. phocator* was discovered feeding on a juvenile neopilionid (unidentifiable to species level) that was clearly freshly killed, rather than scavenged. While without confirmation of species identification, we refrain from terming this cannibalism. However, we observed cannibalism in a laboratory setting, where adult males of *F. bona* killed and consumed other conspecific adult males and sub-adults despite also eating the lab diet. In contrast, adult and subadult *F. pureora* and *P. listeri* were frequently housed in various densities in a lab setting with lab diet we provided, and never engaged in cannibalism. Upon successfully completing a molt, we observed an adult male *P. listeri,* adult male *F. bona*, and a juvenile *F. bona* feeding on their shed exoskeleton (Fig. 6).

Figure 3.—New Zealand Neopilionidae with scavenged arachnid food items. (a) Juvenile *Forsteropsalis pureora* feeding on a leg of the sheet-web spider *Cambridgea* sp. (Desidae) in Waitomo. (b) Adult female *F. pureora* feeding on a leg of the spider *Cycloctenus* sp. (Cycloctenidae) in Waitomo. (c) Adult male *F. inconstans* feeding on scavenged *Cycloctenus* sp. (Cycloctenidae) in Lower Hutt. (d) Adult female *Pantopsalis listeri* feeding on scavenged remains of a short-legged harvestman (Triaenonychidae) in Westland. Photographs (a) and (b) by E.C. Powell, (c) by U. Schneehagen, and (d) by J. Warfel.

Some neopilionids may also eat plant matter, such as detritus or vegetation, but we did not observe this in the field. In captivity, we found that *F. pureora*, *F. bona*, and *P. listeri* readily accepted wet dog food as well as plant matter including apple and carrot (Table 1). Cereal baits delivering sodium monofluoroacetate "1080" to control mammalian pest species (e.g., possums, rats, mice, stoats, and hedgehogs) are commonly deployed across New Zealand (reviewed by Eason et al. 2011). Poison baits are often fed upon by invertebrates and other non-target endemic species. In at least one study, there is a specific mention of individuals of *Megalopsalis* sp. (a genus name which is now valid for only a single species in New Zealand) as a visitor to bait stations, where they consume baits made up of cereals and carrot (see Table 1).

Figure 4.—*Pantopsalis listeri* male and female with scavenged blowfly food. The male began by opening the cuticle of the prey item, exposing the soft integument. He then backed away and the female stepped forward to feed. Photograph by S. Pollard.

Predators.—We directly observed predation of New Zealand neopilionids by multiple species of spider in the field, which adds several new species to the known arachnid predators of Opiliones worldwide (Table 2, Fig. 7). First, we observed two instances where brown vagrant spiders, *Uliodon* sp. (Zoropsidae), consumed freshly killed (still moving) adult males of *F. pureora* (Fig. 7c). We also observed an adult female of the square-ended crab spider, *Sidymella angularis* (Urquhart, 1885) (Thomisidae), with a freshly captured juvenile of *F. chiltoni* (Fig. 7a). Another spider that uses sit-and-wait hunting tactics, the nursery web spider, *Dolomedes minor* L. Koch, 1876 (Pisauridae), captured a male *F. pureora* in Te Rapa, Hamilton (B. McQuillan pers. comm.). Moreover, we observed several neopilionids captured by web-building

Figure 5.—Subadult male *F. inconstans* competing with a *Schedotrigona* sp. millipede over a scavenged amphipod in Lower Hutt. (a) Millipede and harvestman feeding on an amphipod . (b) The harvestman was successful in retaining the scavenged food and moved away from the millipede. Photographs by U. Schneehagen.

spiders, including two separate observations of an adult male of *F. pureora* trapped in the web of the sheet-web spider, *Cambridgea* sp. (Desidae) (Fig. 7d), and an adult male of *P. phocator* trapped in the web of an unidentified araneoid spider (Araneidae or Theridiidae). A web-building pirate spider, *Australomimetus sennio* (Urquhart, 1891) (Mimetidae), captured a female of *F. pureora* in Rotorua (B. McQuillan pers. comm.). An adult male *F. inconstans* was observed being eaten by a cave orbweaver, *Taraire* (=*Meta*) *rufolineata* (Urquhart, 1889) in Kahurangi National Park, Tasman (D. Hegg pers. comm). Finally, in Lower Hutt, Wellington, an adult male of *F. inconstans* was captured and eaten by a cobweb spider, *Theridion zantholabio* Urquhart, 1886 (Theridiidae) (U. Schneehagen pers. comm) (Fig. 7b).

In a literature review of prey records for New Zealand species, we found several vertebrate species (including reptiles, amphibians, birds, and mammals) known to feed on Opiliones, but it was unclear in most studies whether these harvestmen were endemic Neopilionidae, Pettalidae, Triaenonychidae, Synthetonychiidae, *Acropsopilio* Silvestri, 1904, or the introduced *Phalangium opilio* because harvestmen were almost never identified past order level (see Table 2). Most of the species with prey records that included Opiliones showed that harvestmen made up little of the overall diet. In contrast, one study found that the European harvestman *P. opilio* was found in 46% of 53 hedgehog (*Erinaceus europaeus*) stomachs analyzed in New Zealand pastureland (Campbell 1973).

We confirmed that some passerine birds, including the dunnock, *Prunella modularis*, the starling, *Sturnus vulgaris*, and the rook, *Corvus frugilegus*, which are known to feed on harvestmen in Europe (Cokendolpher & Mitov 2007), also feed on harvestmen in New Zealand (Table 2). Furthermore, other invasive species, including hedgehogs, three species of rat, and less importantly, stoats and brushtail possums also include harvestmen in their diet (Table 2). Multiple native species also prey on harvestmen, including the tuatara, *Sphenodon punctatus*, the frog *Leiopelma* sp., an amphibious climbing fish, *Galaxias brevipinnis*, five species of skinks in the genus *Leiolopisma*, the bat *Mystacina tuberculata*, and several bird species such as the kiwi, *Apteryx australis* (Table 2). For most species, the frequency of harvestmen in their diet was low, but for the skinks *L. zealandicum* and *Leiolopisma* sp. harvestmen constituted 14% and 23% of the prey, respectively (Gill 1976).

Defensive behaviors.—Leg autotomy is a frequent defense tactic in neopilionids. We found 55% of individuals missing at least one leg in *F. pureora* in this study ($n = 189$) and 53% missing at least one leg in *P. listeri* ($n = 34$) (S. Pollard unpub. data). Leg autotomy had occurred in individuals of every species we collected from the field, including *F. bona, F. chiltoni*, *F. fabulosa*, *F. inconstans*, *F. marplesi*, *F. photophaga*, *F. pureora*, *M. parvum, P. albipalpis, P. coronata, P. listeri*, and *P. phocator* (Figs. 8a–c), and confirmed for *F. wattsi* using photos provided by D. Hegg (pers. comm). We did not explicitly compare the rates of autotomy among these species,

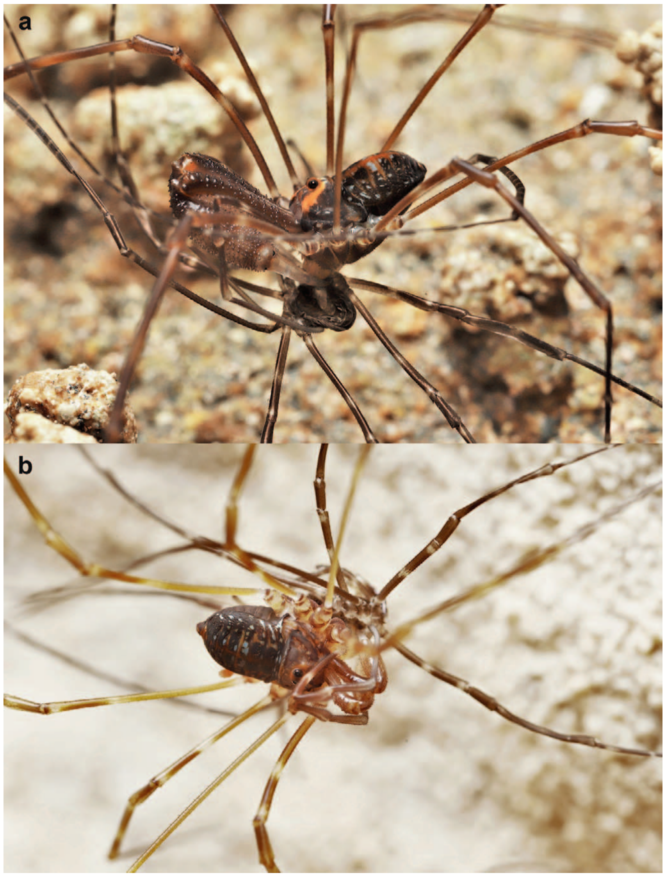

Figure 6.—Cave-dwelling *Forsteropsalis bona* extracting fluids from shed exuviae after molting inside caves in Waitomo, New Zealand. (a) Adult male *F. bona* and (b) juvenile *F. bona*. Both photographs by E.C. Powell.

but we noticed general trends suggesting that the cave-dwelling species, *F. bona* and *F. photophaga*, autotomized legs less frequently than forest-dwelling species.

Upon detecting light, most individuals first attempted to flee. Thanatosis was also employed by all species of Neopilionidae we collected, where harvestmen dropped to the ground with all legs straight up and did not move (Fig. 8d). This behavior usually occurred only after individuals had attempted but failed to flee and was sometimes used in conjunction with leg autotomy. We also found that neopilionids, including *F. pureora* and *P. listeri*, occasionally aggregate in smaller numbers (up to seven at a time) (Fig. 9), but this behavior was never accompanied by bobbing when the individuals were disturbed.

Finally, we detected no chemical defense secretions in New Zealand neopilionids by our direct observation (including close inspection, smelling, and tasting) when individuals of many species were handled, but it is unknown whether there could be chemical defenses that are not perceived by our human sensory systems. The only non-evasive defense we recorded among neopilionids was the attack with their chelicerae during a simulated predator attack with forceps. Females, with reduced chelicerae, seemed to employ this behavior as much as males, which have exaggerated, sexually-selected chelicerae (Figs. 1–4, 9).

DISCUSSION

Diet.—In the first part of this study we provide a list of food items for the New Zealand Neopilionidae using direct observations, iNaturalist records online, and a comprehensive literature review. Previously, only a single food type for the species *Forsteropsalis photophaga* was noted in the literature and nothing was known for the remainder of the neopilionids. We show here that several other New Zealand species in this family are generalist predators, preying and scavenging on a wide variety of invertebrate food items (Table 1). Our findings are consistent with other literature examining the diet of species belonging to the suborders Eupnoi and Laniatores, which are most often generalist predators with a preference for soft-bodied invertebrate food items (reviewed in Acosta & Machado 2007). When scavenging, however, a much wider range of food items can be consumed, including large items that would be difficult or dangerous to subdue alive. Thus, scavenging may confer a great advantage by expanding the food base of the individuals and increasing their energy intake.

The opportunistic aspect of the diet of neopilionids is reinforced by the use of discarded spider prey by *F. pureora* (Table 1). Because spiders feed extra-orally, they discard the exoskeleton of prey items after liquifying and eating their inside (Foelix 2011). Evidence for another potential instance of opportunistic use of a spider's prey, or even potential theft, was observed for a mature male of *F. pureora*. Using photographs, we discovered that a hemipteran food item appeared to be wrapped in silk upon closer inspection (B. McQuillan pers. comm.; Table 1). Although discarded spider prey probably has poor nutritional value, it is used by several other harvestman species (see list in Sabino & Gnaspini 1999). For instance, individuals of *Phalangium opilio* were reported to frequently scavenge on the carcasses of prey discarded by thomisid crab spiders in the United States (Morse 2001). Additionally, a female of *Acutisoma longipes* Roewer, 1913 (Laniatores, Gonyleptidae) was observed stealing a moth directly from a spider (Ctenidae) in Brazil (Sabino & Gnaspini 1999). Discarded spider prey, feces, and other decaying matter may be particularly important in the diet of harvestmen during periods of food shortage, when the availability of potential prey is low.

Neopilionids interacted with heterospecifics, competing for scavenged food items, and with conspecifics, sharing scavenged food items. An observation by S. Pollard suggested that there could be food sharing between sexes in *P. listeri*, where a male provided a female with a food resource. This male behavior could be interpreted as nuptial gift offering, but given the lack of further details, it is unclear. The only known cases of nuptial gifts in harvestmen are glandular secretions, which are produced by the males and transferred to the females via the chelicerae or male genitalia (Martens 1969; Wijnhoven 2011; Fowler-Finn et al. 2018). In the case of neopilionids, males have highly exaggerated chelicerae used for male-male competition (Painting et al. 2015; Powell et al. 2020). Though males and females did not exhibit any striking differences in food size or type (see Table 1), enlarged cheliceral claws could aid males in exposing nutritious food and decrease the time and energy expended by females to get through less nutritious cuticle of invertebrate food items.

Figure 7.—Invertebrate predators of New Zealand Neopilionidae. (a) Female of the square-ended crab spider *Sidymella angularis* (Thomisidae) consuming a juvenile *Forsteropsalis chiltoni* in Oban, Stewart Island. (b) *Forsteropsalis inconstans* male captured and eaten by a female cobweb spider *Theridion zantholabio* (Theridiidae) in Muritai, Lower Hutt. (c) Adult female of the brown vagrant spider *Uliodon* sp. (Zoropsidae) feeding on a male *F. pureora* prey in Ngaruawahia. (d) Adult male *F. pureora* in the web of the sheet-web spider *Cambridgea* sp. (Desidae) in Te Anga. Photographs (a), (c), and (d) by E.C. Powell, and (b) by U. Schneehagen.

Another example of the opportunistic feeding habits of neopilionids is the fact that juveniles and adults of at least two species, *F. bona* and *P. listeri*, feed on their exuvia after molting. Early nymphs of many harvestman species are known to feed on their exuvia after molting or simply to masticate them, which is possibly a strategy to recover water (Gnaspini 2007). To our knowledge, however, there is no reported case of later nymphs and adults of harvestmen feeding on their exuvia. As opportunistic scavengers that will feed on low-quality food when it is available, it is possible that neopilionids use their exuvia as a source of food and not water.

Cannibalism of large juveniles and adults is a rare behavior in harvestmen, and occurs more frequently during the molting cycle, when individuals are less mobile and the tegument is still soft (reviewed in Acosta & Machado 2007). Our observation of *P. phocator* consuming a small juvenile neopilionid in a natural setting follows this trend. Here we also describe cannibalism of adults in *F. bona*, in which adult males killed and consumed other adult males and sub-adults in the laboratory. Cannibalism was not recorded for captive *F. pureora* and *P. listeri*, which were also maintained in the laboratory in variable densities. The occurrence of cannibalism in *F. bona* may be related to the cavernicolous habitat, where food availability is usually limited (Romero 2009). The consumption of vegetal matter was also only recorded in the laboratory, where harvestmen accepted carrot, lettuce, apple, and mango (Table 1). Captive diets of vegetal matter have been tested with harvestmen with varying degrees of success. However, animal matter with high lipid and protein content is most readily accepted overall (reviewed in Acosta & Machado 2007), probably because it promotes greater growth and reproductive output (Naya et al. 2017). Fitting with their preference for animal matter under laboratory conditions, one field study also showed that New Zealand harvestmen were more attracted to poison baits with squid than poison baits without squid (Vergara Parra 2018). There is no evidence that the consumption of sodium monofluoroacetate “1080” causes any direct negative effects to harvestmen or other invertebrates (Spurr & Berben 2004; Powlesland et al. 2005) nor is there evidence that feeding on poison baits indirectly impacts their native (non-mammalian) vertebrate predators, such as birds, lizards, and frogs (Wedding et al. 2010). In fact, all efforts to control and eradicate invasive mammals in New Zealand are likely to benefit endemic harvestmen, because many of the target mammal species are known to prey upon them (see the following section ‘Predators’). In accordance with this prediction, a comparative study showed that harvestmen were more abundant on offshore islands where rats were eliminated than on islands where rats were still present (Bremner et al 1984).

Predators.—In the second part of this study, we provided a list of the predators of New Zealand harvestmen using direct observations in the field and an exhaustive literature review of prey records. We provide the first records of invertebrate

Figure 8.—Predator damage and defense strategies of New Zealand Neopilionidae. (a) Adult male *Forsteropsalis pureora* with broken left chelicera and possible autotomized left leg (2nd pair) in Waitomo. (b) Juvenile *F. bona* missing its left pedipalp and autotomized right leg (1st pair). (c) Adult male *Mangatangi* sp. with two autotomized legs. Legs II and III have been autotomized at different times over the harvestman's life. Leg II was recently autotomized, as evident by the remaining trochanter joint. Leg III was autotomized during the juvenile stages, evident by the missing trochanter and healed cuticle "scar". (d) An adult male *F. pureora* utilizing the defensive posture known as thanatosis. All photographs by E.C. Powell.

predators of Opiliones in the country, including seven spider species and the cannibalism of juveniles and adults (see the previous section 'Diet). The spiders we found to feed on harvestmen were opportunistic generalist predators of invertebrates and are unlikely to specialize on harvestman prey.

In our literature review, we found no prey records for invertebrate predators that included Opiliones, but we did find references for prey records from 32 species of vertebrates. Surprisingly, few of the vertebrate species we found in the literature search were included in the comprehensive review of natural enemies of Opiliones by Cokendolpher & Mitov (2007). Similar to the findings by Cokendolpher & Mitov (2007), we found that most predators were generalists that feed on few harvestmen relative to other taxa. The most important harvestman predators in New Zealand were hedgehogs, rats, and skinks (Campbell 1973; Gill 1976; Sturmer 1988). Information about the types of harvestmen captured was limited because authors almost never identified harvestmen past the order level. Also mirroring the findings by Cokendolpher & Mitov (2007), we found many records of passerine birds as predators of New Zealand harvestmen. While birds likely represent a very important suite of predators, invertebrates are understudied, and their contribution as predators is likely underestimated. This is evident by the fact that we found zero published records of invertebrate predation on New Zealand harvestmen compared to records for nine species of reptiles and amphibians, one record for an amphibious fish, 15 species of birds, and seven species of mammals over 70 years of research. Furthermore, we recognize that gut content and fecal analyses make prey records easier to acquire for vertebrates than invertebrates. This taxonomic bias parallels the exaggerated bias towards bird research and conservation in New Zealand, as well as the extensive studies that have attempted to quantify the impact of invasive mammal species in New Zealand.

An interesting addition to the known predators of Opiliones which was not included in the worldwide review by Cokendolpher & Mitov (2007) is a species of fish. Specifically, Opiliones were identified in the gut contents of climbing galaxias fish (kōaro) in Westland streams (Main & Winterbourn 1987; Table 2). While disparate habitats of aquatic fish and terrestrial harvestmen make it seem unlikely for these taxa to interact, the biology of this fish species and the habitat use of neopilionids explains this finding. Climbing galaxias are amphibious and able to climb steep, slick waterfalls, rock faces, and dams. Forest-dwelling Neopilionidae, especially

Figure 9.—(a) Aggregation of sexually mature *Pantopsalis listeri* in Westland, South Island, New Zealand. On the left, four adult males and on the right, two females (with more cryptic coloration). (b) Two sexually mature male *Forsteropsalis pureora* at Waioeka Gorge, Bay of Plenty. Photograph (a) by J. Warfel and (b) by C.J. Painting.

members of the genus *Forsteropsalis*, are often associated with aquatic environments such as streams, waterfalls, dams, and gorges, and it is plausible that these species would be encountered by climbing fish. For instance, we have found *F. fabulosa* in rock wall crevices receiving spray from nearby waterfalls and have commonly encountered *F. bona, F. pureora,* and *F. marplesi* resting on and around the banks of streams day and night.

Passerine birds were the most frequent predators found to feed on harvestmen in our literature review, including introduced and native species (Table 2). However, harvestmen were never reported as a significant portion of the diet of any bird species. The pattern reported for birds is similar to that of the endemic New Zealand bat, *Mystacina tuberculata,* which consumed Opiliones at several sites, but this prey type is never a significant part of its diet (Arkins et al. 1999; Lloyd 2001). Invasive mammals that feed on harvestmen in New Zealand included three species of rats, hedgehogs, and less importantly, stoats and brushtail possums (Table 2). Rats are significant predators of invertebrate prey in New Zealand, but the importance of harvestmen as prey identified in the literature is mixed. In some studies, spiders were noted as prey, but no

Opiliones were reported at all (Daniel 1973; Gales 1982; Miller & Miller 1995). It is also possible that biologists unfamiliar with arachnids identifying prey from vertebrate gut contents could mistake harvestman legs as those of spiders, thus potentially underrepresenting the order in prey records. In another study on Stewart Island, Opiliones were the second most important invertebrate prey item of rats after wētā (Orthoptera) (Sturmer 1988). Though Opiliones were not identified past order level, Stewart Island is a largely undisturbed habitat covered mostly by native forest. Given our own personal observations, Neopilionidae are much more abundant than other harvestmen on the island and were likely to be the main harvestman group found in rat stomachs in this study.

Defensive behaviors.—In the third part of this study, we describe the defensive behavior of several neopilionid species from New Zealand. Leg autotomy, which is typical defensive behavior recorded for species of Eupnoi (reviewed in Gnaspini & Hara 2007), was also recorded for all neopilionid species here. The frequency of individuals with autotomized legs in two forest-dwelling species, namely *F. pureora* and *P. listeri*, was very high (55% and 53% respectively) and comparable to other species of the family Sclerosomatidae (Eupnoi) that also inhabit forests, such as *Leiobunum nigripes* Weed, 1892 (47%, Guffey 1998), *L. vitattum* (Say, 1821) (45%, Guffey 1998), *L. formosum* (Wood, 1870) (61%, Houghton et al. 2011), *L. politum* Weed, 1890 (36%, Houghton et al. 2011), and *Prionostemma* ssp. (71%, Domínguez et al. 2016). If the frequency of leg autotomy in the two cavernicolous species, namely *F. bona* and *F. photophaga*, is indeed lower than the species that live in the forest, we can infer that the predation pressure on neopilionids inside the cave is likely lower than in the outside environment. In support of this suggestion, most predators recorded in Table 2, including both invertebrates and vertebrates, live exclusively outside caves according to our observations (with exceptions only for occasional *Cambridgea* spp. spiders, *Taraire rufolineata* spiders, and sometimes, rats). In addition to predator encounters, it is also possible that complex forest habitats present more opportunities for legs to become entrapped and autotomized.

Other defensive behavior commonly recorded in many species of Eupnoi from temperate regions is gregariousness, in which as many as 70,000 individuals can be found forming mass aggregations in sheltered areas (reviewed in Machado & Macías-Ordóñez 2007). Here we recorded small aggregations with no more than seven individuals. Although it is not clear whether defense is the main function of harvestman aggregations, individuals may dilute the individual risk of predation in groups (Machado et al. 2000), and this possibility may also apply to the neopilionids studied here. Moreover, when disturbed, the individuals of several species of the family Sclerosomatidae may collectively release scent gland secretions that repel potential predators, and exhibit bobbing behavior, which spreads an alarm signal through the entire aggregation (Holmberg et al. 1984). In the case of the neopilionids, these two defensive behaviors were never recorded, and can be ruled out as potential defensive benefits of aggregations. In fact, the small number of individuals, the male-biased sex composition of the aggregations (Fig. 9) (E.C. Powell unpub. data), and the fact that aggregations are composed of a single layer of individuals with little leg overlapping indicate that the aggregations of New Zealand neopilionids are markedly different from the mass aggregations observed in some Eupnoi from temperate regions. Two North American species, namely *Leiobunum longipes* Menge, 1854 and *L. vittatum* (Sclerosomatidae), form similar loose aggregations in the beginning of the mating season where males encounter females and attempt to copulate (Edgar 1971). Although we never observed mating activity close to the aggregations, we suppose that gregariousness in neopilionids may be more related to mating than to defense.

Surprisingly, we recorded thanatosis in all neopilionid species studied here. To our knowledge, thanatosis in harvestmen is restricted to the suborders Dyspnoi and Laniatores, with several records in the families Dicranolasmatidae, Trogulidae, Cosmetidae, Escadabiidae, Gonyleptidae, Manaosbiidae, Tricommatidae, and Stynopsidae (Gnaspini & Hara 2007; Machado & Pomini 2008; Pomini et al. 2010). In most of these families, the individuals are short-legged and the posture during thanatosis include leg retraction over the body (see Fig. 10.1a,e in Gnaspini & Hara 2007 and Fig. 1b in Pomini et al. 2010). Combined with a dark body coloration, leg retraction may render the individuals in thanatosis more difficult to spot among the leaf litter. In the case of neopilionids, the long legs prevent leg retraction over the body in the same way; instead we found that individuals fully straightened the legs and held them together over the body (Fig. 8d). The dark (usually black or brown) coloration of the New Zealand neopilionids may also make the individuals in thanatosis camouflaged after they fall from the vegetation. Despite this similarity, we suggest that thanatosis in the family Neopilionidae evolved independently from the other suborders of Opiliones, being a unique defensive behavior in the suborder Eupnoi.

Conclusions.—Basic information on natural history of any species is an important first step for other types of studies, such as experimental manipulations and comparative analyses. In the case of harvestmen, natural history data are scarce and highly concentrated in a few genera (e.g., *Leiobunum* CL Koch, 1839) and subfamilies (e.g., Goniosomatinae). Here we provide information on diet, predators, and defensive behaviors of a so-far poorly studied harvestman family that is highly diverse in New Zealand, the Neopilionidae. We showed that the diet of the neopilionids is opportunistic and similar to that of other species of Eupnoi and Laniatores, including both live and dead food items, and also a small portion of vegetal matter. We found cannibalism occurred but was infrequent and experienced mostly by juveniles, as reported for other harvestmen species. We also described instances of opportunistic scavenging using discarded spider prey, competition over scavenged food with heterospecifics, and food sharing by groups of females and between potential mate pairs. The predators of the neopilionids include a great variety of invertebrates and vertebrates, with spiders and passerine birds being the most frequent predators of New Zealand harvestmen—a pattern that has already been reported for other harvestman species worldwide (Cokendolpher & Mitov 2007). Not surprisingly, European birds and mammals that are known to prey on harvestmen in their natural ranges also feed on harvestmen after their introduction in New

Zealand. Finally, the defensive repertoire of neopilionids includes typical behaviors previously recorded for other species of Eupnoi, such as leg autotomy, fleeing, and gregariousness, but also unique behaviors that are only known for species of Dyspnoi and Laniatores, such as thanatosis.

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LITERATURE CITED

Acosta LE, Machado G. 2007. Diet and foraging. Pp. 309–338. *In* Harvestmen: the Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G, eds.), Harvard University Press, Cambridge, MA.

Arkins AM, Winnington AP, Anderson, S, Clout MN. 1999. Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). *Journal of Zoology* 247:183–187.

Barlow M, Moeed A. 1980. Nestling foods of the South Island fernbird (*Bowdleria punctata punctata*). *Notornis* 27:68.

Benson TJ, Chartier NA. 2010. Harvestmen as predators of bird nestlings. *Journal of Arachnology* 38:374–377.

Berland L. 1949. Ordre des opilions. *Traité de Zoologie* 6:761–793.

Boyer SL, Giribet G. 2009. Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography* 36:1084–1099.

Bremner AG, Butcher CF, Patterson GB. 1984. The density of indigenous invertebrates on three islands in Breaksea Sound, Fiordland, in relation to the distribution of introduced mammals. *Journal of the Royal Society of New Zealand* 14:379–386.

Broadley RA. 2012. Notes on pupal behaviour, eclosion, mate attraction, copulation and predation of the New Zealand glowworm *Arachnocampa luminosa* (Skuse) (Diptera: Keroplatidae), at Waitomo. *New Zealand Entomologist* 35:1–9.

Brockie RE. 1990. European hedgehog. Pp. 99–113. *In* The Handbook of New Zealand Mammals (King CM, ed.). Oxford University Press, Oxford.

Campbell PA. 1973. The feeding behaviour of the hedgehog (*Erinaceus europaiws* L.) in pastureland in New Zealand. *Proceedings of the New Zealand Ecological Society* 20:35–40.

Castanho LM, Rocha RD. 2005. Harvestmen (Opiliones: Gonyleptidae) predating on treefrogs (Anura: Hylidae). *Revista Ibérica de Aracnología* 11:43–45.

Clapperton BK, Maddigan F, Chinn W, Murphy EC. 2019. Diet, population structure and breeding of *Rattus rattus* L. in South Island beech forest. *New Zealand Journal of Ecology* 43:1–8.

Cokendolpher JC, Mitov PG. 2007. Natural enemies. Pp. 339–373. *In* Harvestmen: the Biology of Opiliones (Pinto-da-Rocha R, Machado G, Giribet G, eds.). Harvard University Press, Cambridge, MA.

Cowan PE, Moeed A. 1987. Invertebrates in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp/broadleaf forest, Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Zoology* 14:163–177.

Cramp S, Perrins CM. (eds.) 1994. The Birds of the Western Palearctic. Vol. VIII. Crows to Finches. Oxford University Press, Oxford.

Curtis DJ, Machado G. 2007. Ecology. Pp. 280–308. *In* Harvestmen: the Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G, eds.), Harvard University Press, Cambridge, MA.

Daniel M. 1973. Seasonal diet of the ship rat (*Rattus r. rattus*) in lowland forest in New Zealand. *Proceedings of the New Zealand Ecological Society* 20:21–30.

Dick AMP. 1985. Rats on Kapiti Island, New Zealand: coexistence and diet of *Rattus norvegicus* Berkenhout and *Rattus exulans* Peale. MSc thesis. Massey University, New Zealand.

Domínguez M, Escalante I, Carrasco-Rueda F, Figuerola-Hernández CE, Ayup MM, Umaña, MN et al. 2016. Losing legs and walking hard: effects of autotomy and different substrates in the locomotion of harvestmen in the genus *Prionostemma*. *Journal of Arachnology* 44:76–83.

Edgar AL. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). *Miscellaneous Publications Museum of Zoology, University of Michigan*. 44:1–68.

Edmunds M. 1974. Defence in Animals: A Survey of Anti-predator Defences. Longman, Harlow, Essex.

Eason C, Miller A, Ogilvie S, Fairweather A. 2011. An updated review of the toxicology and ecotoxicology of sodium fluoroacetate (1080) in relation to its use as a pest control tool in New Zealand. *New Zealand Journal of Ecology* 35:1–20.

Fleming PA, Muller D, Bateman PW. 2007. Leave it all behind: a taxonomic perspective of autotomy in invertebrates. *Biological Reviews* 82:481–510.

Foelix RF. 2011. Biology of Spiders. Oxford University Press, New York, NY.

Forster RR. 1947. The zoogeographical relationships of the New Zealand Opiliones. *The New Zealand Science Congress* 233–235.

Forster RR. 1948. A new genus and species of the family Acropsopilionidae (Opiliones) from New Zealand. *Transactions of the Royal Society of New Zealand* 77:139–141.

Forster RR. 1954. The New Zealand harvestmen (sub-order Laniatores). *Canterbury Museum Bulletin* 2:1–329.

Fowler-Finn K, Boyer S, Ikagawa R, Jeffries T, Kahn et al. 2018. Variation in mating dynamics across five species of leiobunine harvestmen (Arachnida: Opliones [sic]). *Biology* 7:36.

Gales RP. 1982. Age-and sex-related differences in diet selection by *Rattus rattus* on Stewart Island, New Zealand. *New Zealand Journal of Zoology* 9:463–466.

Gill BJ. 1976. Aspects of the ecology, morphology, and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. *New Zealand Journal of Zoology* 3:141–157.

Gill BJ. 1980. Foods of the longtailed cuckoo. *Notornis* 27:96.

Gnaspini P. 1996. Population ecology of *Goniosoma spelaeum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). *Journal of Zoology* 239:417–435.

Gnaspini P. 2007. Development. Pp. 455–472. *In* Harvestmen: the Biology of Opiliones (Pinto-da-Rocha R, Machado G, Giribet G, eds.). Harvard University Press, Cambridge, MA.

Gnaspini P, Hara MR. 2007. Defense mechanisms. Pp. 374–399. *In* Harvestmen: the Biology of Opiliones (Pinto-da-Rocha R, Machado G, Giribet G, eds.). Harvard University Press, Cambridge, MA.

Guffey C. 1998. Leg autotomy and its potential fitness costs for two species of harvestmen (Arachnida, Opiliones). *Journal of Arachnology* 26:296–302.

Gurr L. 1952. Some food of the North Island kiwi (*Apteryx australis*). *Notornis* 4:209–210.

Halaj J, Cady AB. 2000. Diet composition and significance of earthworms as food of harvestmen (Arachnida: Opiliones). *American Midland Naturalist* 143:487–491.

Haw JM, Clout MN. 1999. Diet of morepork (*Ninox novaeseelandiae*) throughout New Zealand by analysis of stomach contents. *Notornis* 46:333–345.

Haw JM, Clout MN, Powlesland RG. 2001. Diet of moreporks (*Ninox novaeseelandiae*) in Pureora Forest determined from prey remains in regurgitated pellets. *New Zealand Journal of Ecology* 25:61–67.

Holmberg RG, Angerilli NP, LaCasse LJ. 1984. Overwintering aggregations of *Leiobunum paessleri* in caves and mines (Arachnida, Opiliones). *Journal of Arachnology* 12:195–204.

Hopkin SP, Read HJ. 1992. The Biology of Millipedes. Oxford University Press, Oxford.

Houghton JE, Townsend VR, Proud DN. 2011. The ecological significance of leg autotomy for climbing temperate species of harvestmen (Arachnida, Opiliones, Sclerosomatidae). *Southeastern Naturalist* 10:579–591.

Humphreys RK, Ruxton GD. 2018. A review of thanatosis (death feigning) as an anti-predator behaviour. *Behavioral Ecology and Sociobiology* 72:22.

Jeffries D. 2011. Ecology and behaviour of the European hedgehog (*Erinaceus europaeus*) in coastal ecosystems of the greater Auckland region. Doctoral dissertation, University of Auckland.

Komposch C. 1992. Morphologie, Verbreitung und Bionomie des Weberknechtes *Anelasmocephalus hadzii* Martens, 1978 (Arachnida, Opiliones). Diplomarbeit, Naturwissenschaftliche Fakultät, Universität Graz, Austria.

Lloyd BD. 2001. Advances in New Zealand mammalogy 1990–2000: short-tailed bats. *Journal of the Royal Society of New Zealand* 31:59–81.

Machado G, Macías-Ordóñez R. 2007. Social behavior. Pp. 400–413. *In* Harvestmen: the Biology of Opiliones. (Pinto-da-Rocha R, Machado G, Giribet G, eds.), Harvard University Press, Cambridge, MA.

Machado G, Pizo MA. 2000. The use of fruits by the neotropical harvestman *Neosadocus variabilis* (Opiliones, Laniatores, Gonyleptidae). *Journal of Arachnology* 28:357–361.

Machado G., Pomini AM. 2008. Chemical and behavioral defenses of the neotropical harvestman *Camarana flavipalpi* (Arachnida: Opiliones). *Biochemical Systematics and Ecology* 36:369–376.

Machado G, Pinto-da-Rocha R, Giribet G. 2007. What are harvestmen? Pp. 1–13. *In* Harvestmen: the Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.), Harvard University Press, Cambridge, MA.

Machado G, Raimundo RLG, Oliveira PS. 2000. Daily activity schedule, gregariousness, and defensive behaviour in the Neotropical harvestman *Goniosoma longipes* (Opiliones: Gonyleptidae). *Journal of Natural History* 34:587–596.

Main MR, Winterbourn MJ. 1987. Diet and feeding of koaro (*Galaxias brevipinnis*) in forested South Westland streams. *Mauri Ora* 14:77–86.

Marples BA. 1942. Study of the little owl, *Athene noctua*, in New Zealand. *Transactions of the Royal Society of New Zealand* 72:237–252.

Martens J. 1978. Weberknechte, Opiliones. *Die Tierwelt Deutschlands* 64:1–464.

Martens J. 1969. Die Sekretdarbietung während des Paarungsverhaltens von *Ischyropsalis* C. L. Koch (Opiliones). *Zeitschrift für Tierpsychologie* 26:513–523.

Meyer-Rochow VB, & Liddle AR. 1988. Structure and function of the eyes of two species of opilionid from New Zealand glow-worm caves (*Megalopsalis tumida*: Palpatores, and *Hendea myersi cavernicola*: Laniatores). *Proceedings of the Royal Society of London. Series B, Biological Sciences* 233:293–319.

Miller CJ, Miller TK. 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology* 19:19–27.

Moeed A. 1976. Birds and their food resources at Christchurch international airport, New Zealand. *New Zealand Journal of Zoology* 3:373–390.

Moeed A. 1979. Foods of the silvereye (*Zosterops lateralis*; Aves) near Nelson, New Zealand. *New Zealand Journal of Zoology* 6:475–477.

Moeed A. 1980. Diets of adult and nestling starlings (*Sturnus vulgaris*) in Hawke's Bay, New Zealand. *New Zealand Journal of Zoology* 7:247–256.

Moeed A, Fitzgerald BM. 1982. Foods of insectivorous birds in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Zoology* 9:391–403.

Moore SJ, Battley PF, Henderson IM, Webb CL. 2006. The diet of brown teal (*Anas chlorotis*). *New Zealand Journal of Ecology* 30:397–403.

Morse DH. 2001. Harvestmen as commensals of crab spiders. *Journal of Arachnology* 29:273–276.

Naya DE, Lardies MA, Bozinovic F. 2017. Physiological and life-history plasticity in a harvestman species: contrasting laboratory with field data. *Annales Fennici* 54:293–301.

Nottingham CM, Glen AS, Stanley MC. 2019. Snacks in the city: the diet of hedgehogs in Auckland urban forest fragments. *New Zealand Journal of Ecology* 43:1–8.

Pabst W. 1953. Zur Biologie der mitteleuropäischen Troguliden. *Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere* 82:1–46.

Painting CJ, Probert AF, Townsend DJ, Holwell GI. 2015. Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. *Scientific Reports* 5:16368.

Patterson GB. 1992. The ecology of a New Zealand grassland lizard guild. *Journal of the Royal Society of New Zealand* 22:91–106.

Pomini AM, Machado G, Pinto-da-Rocha R, Macías-Ordóñez R, Marsaioli AJ. 2010. Lines of defense in the harvestman *Hoplobunus mexicanus* (Arachnida: Opiliones): Aposematism, stridulation, thanatosis, and irritant chemicals. *Biochemical Systematics and Ecology* 38:300–308.

Porter RER. 1979. Food of the rook (*Corvus frugilegus* L.) in Hawke's Bay, New Zealand. *New Zealand Journal of Zoology* 6:329–337.

Powell EC, Painting CJ, Hickey AJ, Holwell GI. 2020. Defining an intrasexual male weapon polymorphism in a New Zealand harvestman (Opiliones: Neopilionidae) using traditional and geometric morphometrics. *Biological Journal of the Linnean Society* 130: 395–409.

Powlesland RG, Stringer IAN, Hedderley D. 2005. Effects of an aerial 1080 possum poison operation using carrot baits on invertebrates in artificial refuges at Whirinaki Forest Park, 1999–2002. *New Zealand Journal of Ecology* 29:193–205.

Pugsley C. 1984. Ecology of the New Zealand glowworm, *Arachnocampa luminosa* (Diptera: Keroplatidae), inthe glowworm cave, Waitomo. *Journal of the Royal Society of New Zealand* 14:387–407.

Richards ALM. 1960. Observations on the New Zealand glow-worm *Arachnocampa luminosa* (Skuse) 1890. *Transactions of the Royal Society of New Zealand* 88:559–574.

Rickard CG. 1996. Introduced small mammals and invertebrate conservation in a lowland podocarp forest, South Westland, New Zealand. MSc thesis. University of Canterbury, New Zealand.

Romero A. 2009. Cave Biology: Life in Darkness. Cambridge University Press.

Sabino J, Gnaspini P. 1999. Harvestman (Opiliones, Gonyleptidae) takes prey from a spider (Araneae, Ctenidae). *Journal of Arachnology* 27:675–678.

Sankey JHP. 1949. Observations on the food, enemies and parasites of British harvest-spiders (Arachnida, Opiliones). *Entomologist's Monthly Magazine* 85:246–247.

Schaus MH, Townsend VR, Illinik JJ. 2013. Food choice of the Neotropical harvestman *Erginulus clavotibialis* (Opiliones: Laniatores: Cosmetidae). *Journal of Arachnology,* 41:219–222.

Shaw SD, Skerratt LF, Kleinpaste R, Daglish L, Bishop PJ. 2012. Designing a diet for captive native frogs from the analysis of stomach contents from free-ranging *Leiopelma*. *New Zealand Journal of Zoology* 39:47–56.

Sherley G, Wakelin M, McCartney P. 1999. Forest invertebrates found on baits used in pest mammal control and the impact of sodium monofluoroacetate ("1080") on their numbers at Ohakune, North Island, New Zealand. *New Zealand Journal of Zoology* 26:279–302.

Spurr EB, Berben PH. 2004. Assessment of non-target impact of 1080-poisoning for vertebrate pest control on weta (Orthoptera: Anostostomatidae and Rhaphidophoridae) and other invertebrates in artificial refuges. *New Zealand Journal of Ecology* 28:63–72.

Sturmer AT. 1988. Diet and coexistence of *Rattus rattus rattus* (Linnaeus), *Rattus exulans* (Peale) and *Rattus norvegicus* (Berkenhout) on Stewart Island, New Zealand. MSc thesis. Massey University, New Zealand.

Taylor CK. 2004. New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae)–the genus *Pantopsalis*. *Tuhinga* 15:53–76.

Taylor CK. 2011. Revision of the genus *Megalopsalis* (Arachnida: Opiliones: Phalangioidea) in Australia and New Zealand and implications for phalangioid classification. *Zootaxa* 2773:1–65.

Taylor CK, Probert A. 2014. Two new species of harvestmen (Opiliones, Eupnoi, Neopilionidae) from Waitomo, New Zealand. *ZooKeys* 434:37–45.

Tomek T. 1988. The breeding biology of the Dunnock *Prunella modularis modularis* (Linnaeus, 1758) in the Ojców National Park (South Poland). *Acta Zoologica Cracoviensia* 31:1–10.

Ussher GT. 1999. Tuatara (*Sphenodon punctatus*) feeding ecology in the presence of kiore (*Rattus exulans*). *New Zealand Journal of Zoology* 26:117–125.

Vélez S, Fernández R, Giribet G. 2014. A molecular phylogenetic approach to the New Zealand species of Enantiobuninae (Opiliones: Eupnoi: Neopilionidae). *Invertebrate Systematics* 28:565–589.

Vergara Parra OE. 2018. Macroinvertebrate community responses to mammal control-Evidence for top-down trophic effects. Doctoral dissertation. Victoria University of Wellington, New Zealand.

Walls GY. 1981. Feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island, Cook Strait. *New Zealand Journal of Ecology* 4:89–97.

Wedding CJ, Ji W, Brunton DH. 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.

Wijnhoven H. 2011. Notes on the biology of the unidentified invasive harvestman *Leiobunum* sp. (Arachnida: Opiliones). *Arachnologische Mitteilungen* 41:7–30.

Wolff JO, Schönhofer AL, Martens J, Wijnhoven H, Taylor CK, Gorb SN. 2016. The evolution of pedipalps and glandular hairs as predatory devices in harvestmen (Arachnida, Opiliones). *Zoological Journal of the Linnean Society* 177:558–601.

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