# Chapter 6
# The Ecology of New Zealand's Lizards

**Kelly M. Hare, David G. Chapple, David R. Towns, and Dylan van Winkel**

**Abstract** The current distribution of New Zealand lizards has been influenced by past geological events, habitat destruction and introduced predators. Perhaps as a reflection of long isolation, and at least 20 million years of climatic and geological change, the proportion of lizard species that are habitat generalists is relatively low, and high levels of sympatry exist in many environments. Variable strategies in resource partitioning may enable the high sympatry among lizard species, enabling division of resources spatially, temporally and/or trophically. However, overlap in resource use exists, such as honeydew sources, indicating potential competition among and within species. Compared to lizards elsewhere, the New Zealand lizard fauna has some unusual traits, with many species that reside in relatively cool environments, including some that appear to be alpine specialists, some skinks being active at night and *Naultinus* geckos being day active (geckos are globally dominated by nocturnal species). The lizards of New Zealand are highly opportunistic, responding to fluctuating abundance and availability of dietary items throughout the year. Both taxa feed primarily on arthropods, with plant-derived material, other reptiles and carrion also present in the diet; skinks also eat other invertebrates. Both the skinks and geckos of New Zealand disperse seeds and are probably pollinators for some plants. Some New Zealand lizards form aggregations and/or family groupings, and parental care may also be present. Some species use habitat differently in the presence of predators, which include native and introduced birds and invertebrates, native reptiles and introduced amphibians and reptiles.

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D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_6

**Keywords** Behaviour • Diet • Gecko • Habitat use • Mating behaviour • Pollination • Predation • Seed dispersal • Skink

## 6.1 Introduction

Ecology is an interdisciplinary field that includes all branches of biology, plus elements of geography and the earth sciences, but focusses in particular on the interactions among organisms and their environment (Molles 2013). Ecological data, distribution, habitat use, trophic interactions and behavioural responses, are useful for most disciplines in the biological sciences, but in particular are required for effective conservation management. With at least 61 extant species of skinks (Scincidae) and 43 species of gecko (Diplodactylidae), New Zealand has the most diverse lizard assemblage of any temperate archipelago (here species refers to both described and undescribed entities; Daugherty et al. 1990; Hitchmough et al. 2016a, b). Lizards have been present in New Zealand since the Eocene-Oligocene (geckos) or Miocene (skinks) (Worthy 2016; Chapple and Hitchmough 2016), living in an environment that not only had a different vegetation structure, but was completely free of introduced mammalian predators and terrestrial snakes (Chapple and Hitchmough 2016). These historical factors, coupled with many species showing strategies such as late maturity and low annual reproductive output (Cree and Hare 2016; Cree 1994), make New Zealand's lizards particularly vulnerable to novel external influences. Most lizards of New Zealand have undergone large-scale range contractions since human settlement (~1000 ya), through a combination of effects from habitat modification and predation by introduced fauna, especially mammals (Towns et al. 2016). As such, many species require direct conservation management (Tingley et al. 2013), for which knowledge of their ecology is vital.

This chapter examines the ecological characteristics of New Zealand's lizards, including their distribution, habitat use, behaviour and trophic interactions (inter- and intraspecific interactions, diet and predators). We note that many factors important to understanding the ecology of New Zealand's lizards are outlined elsewhere in this volume; here, we may touch on them briefly but will ultimately refer the reader to the other chapters. Our aims in undertaking this review are to: (1) provide a broad overview of several key aspects of lizard ecology in New Zealand, and (2) to indicate any areas that particularly require further investigation. We preferentially use data from wild populations, noting where data are from captive sources. We do not aim to be comprehensive in coverage, instead we point the reader to primary literature and more in-depth studies. However, we do attempt to outline various differences in the ecology of skinks and geckos within a New Zealand context, and compare them with similar species overseas.

## 6.2 Distribution, Habitat Use, Sympatry and Resource Partitioning

### *6.2.1 Distribution and Habitat Types Within New Zealand's Islands*

New Zealand is a long narrow archipelago of over ~650 islands spanning ~1600 km along a north-northeast axis, with a maximum land width of ~400 km. Altitude ranges from 0 m a.s.l along the extensive coastline of New Zealand (~15000 km) to mountain peaks reaching 3754 m a.s.l (Gibbs 2006; Neall and Trewick 2008). Prior to human settlement (~1000 ya), lizards were found throughout all islands of New Zealand, except the near sub-tropical Kermadec Islands and the Sub-Antarctic Islands (Worthy 2016). Although much reduced in range, species of skinks and geckos are still present throughout the mainland and offshore islands from the Three Kings Islands north of North Island to Rakiura/Stewart Island in the far south; latitudes from 34 to 47°S (Chapple and Hitchmough 2016). Distribution among habitats is similarly broad, with some lizard species from both families found in environments ranging from coastal beaches (0 m a.s.l) to alpine scrub and scree (~2200 m a.s.l) and from forest to regenerating scrub to tussock grasslands. Some species are also present in what might be termed marginal habitats, on offshore rock stacks, in modified agricultural lands and/or in urban settings (e.g. Barwick 1959; Liggins et al. 2008; Reardon et al. 2012). Although a few species (~7 %) could be termed as generalist in their habitat distribution (e.g. present from the coast to subalpine regions; Fig. 6.1a, b), most can be classified into more defined geographic distributions. For example, some *Oligosoma* are only found along the coastal shoreline (e.g. *O. suteri* and *O. acrinasum*; Towns 1975; Thomas 1985) and some only in alpine regions (e.g. *Mokopirirakau kahutarae*, Whitaker 1984). Interestingly, no geckos have been observed to be strictly coastal, whereas five species of skinks are classified as coastal dwellers, inhabiting the shoreline and sometimes entering coastal scrub (Towns et al. 1985). As more data are obtained on the distributions of species, it is likely that habitat classifications will alter and that more refined habitat classifications will be possible.

### *6.2.2 Sympatry and Resource Partitioning*

Environmental resources are generally partitioned in three main ways, temporally, spatially and trophically, that is, by time of activity, spaces used and/or foods eaten (Whitaker 1968; Towns et al. 1985). Resource partitioning reduces competition and is probably how many species can coexist (e.g. Towns et al. 1985; Box 6.1). However, when only one potential resource partitioning character is used, character displacement among species may not be found. For example, Montoya and Burns (2007) concluded that where little support was found for character displacement

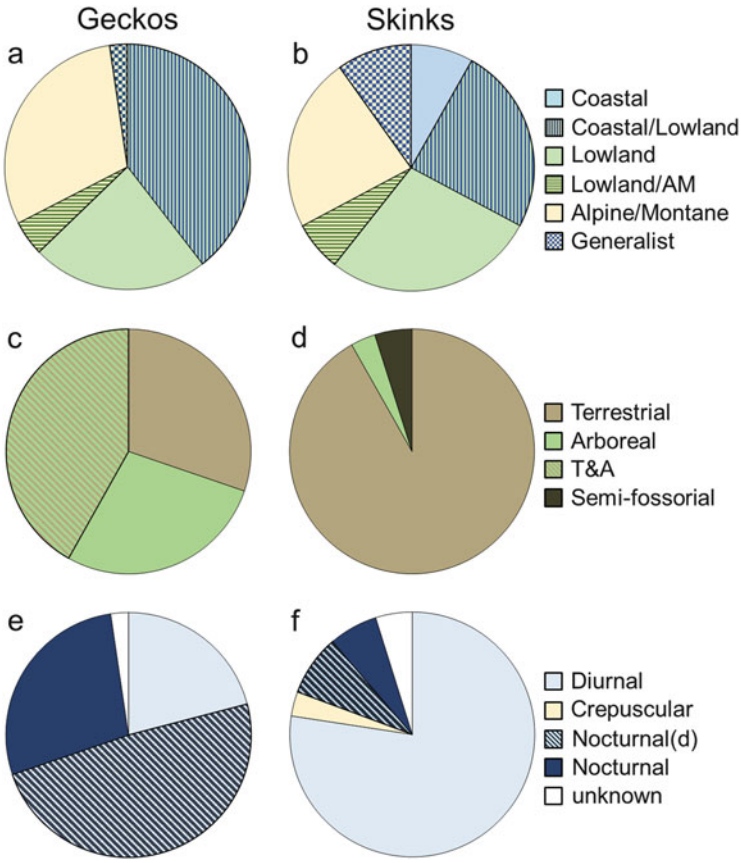


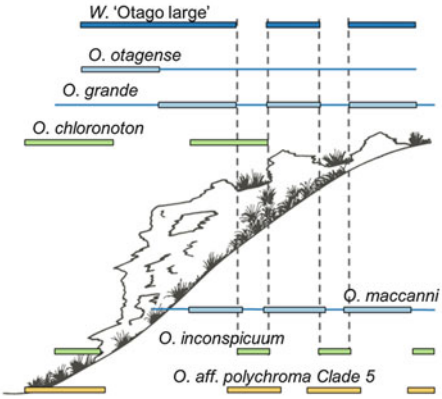

**Fig. 6.1** Habitat use and activity times of endemic gecko ($N = 43$) and skink species ($N = 61$) from New Zealand. *Top row*. Biogeographic affinity for: (**a**) geckos and (**b**) skinks. Coastal = 0–50 m a.s.l; lowland = 50–500 m a.s.l; alpine/montane (AM) ≥ 500 m; generalist = present from coast to alpine regions. *Middle row*. Habitat use for: (**c**) geckos and (**d**) skinks. Terrestrial = found on ground; arboreal = found in trees/scrub (may use terrestrial retreats); T&A = uses both terrestrial and arboreal structures; semi-fossorial = terrestrial species that uses burrows and leaf litter. *Bottom row*. Main activity/foraging times for: (**e**) geckos and (**f**) skinks. Diurnal = diurnally foraging; crepuscular = dawn and dusk foraging (NB both crepuscular skink species have also been seen basking by day); nocturnal (d) = nocturnally foraging species seen basking by day; nocturnal = nocturnally foraging. Data and groupings are based on Tingley et al. (2013); with some additional data since 2013 available from the corresponding author on request. *Note*: these charts show general trends and should not be used as absolute values (see text for more explanation)

(due to body size and diet preference) on some islands, other factors, such as interspecific differences in habitat selection and/or diurnal activity patterns, may interact with differences in prey size selection to promote coexistence among *Oligosoma* skinks.

## Box 6.1 Resource partitioning

The lizards of New Zealand have a high level of sympatric species diversity, most likely through resource partitioning at temporal, spatial and trophic scales (i.e. time of activity, spaces used, and/or foods eaten). One surprisingly diverse lizard fauna is among the fractured schist rock outcrops (tors) and steep gullies of the Otago high country (see diagram and references cited within), where seven lizard species may be found on or near each tor.

The only nocturnally foraging species is the gecko *W.* 'Otago large' which by day may form large aggregations under rock plates and in rock crevices. The largest skink species, *Oligosoma otagense,* most commonly uses fractured sunny rock faces on bluffs, and the smaller *O. grande* are more common on exposed and isolated tors. Similar in size to *O. grande* are *O. chloronoton*, which may occasionally bask, but are most active on large tors in the cooler months of spring moving in the hot summer months to cooler vegetated gullies. Of the three smaller skinks, *O. maccanni* is commonly found under rocks near the base of tors, and may use herbs and shrubs, the rarely seen *O. inconspicuum* is usually associated with vegetated gullies and damper areas, preferring herbs and shrubs, and *O.* aff. *Polychroma* Clade 5 occasionally bask on tors, but more commonly inhabit grasslands. Dietary separation may exist among the skinks which vary in size, and also alter food preference seasonally (see section 6.3). Further north, even more diverse, but spatially constrained lizard assemblages exist on some islands (Towns et al. 1985). For example, on Middle Island, Mercury Island Group, 10 lizard species are segregated spatially as terrestrial, arboreal, or burrow-inhabiting, as well as by time of activity and size.




Habitat use of lizards in subalpine tussock grasslands of Central Otago. Habitats used often are shown by solid bars, with solid connecting lines indicating less-used habitats. Blue = saxicolous/rock dwelling; Green = herbs and shrubs; Gold = tussock grasslands. Figure modified with permission from Towns et al. 1985 © Royal Society of New South Wales, updated using Patterson and Daugherty 1990, Berry et al. 2005, R. Mules pers comm.

**Box 6.1** Resource partitioning

Despite the varied habitat distribution among New Zealand lizards, sympatric species diversity is unusually high for a temperate region (Towns and Daugherty 1994; Chapple et al. 2011). Local assemblages may comprise large numbers of lizard species (Towns and Daugherty 1994), and one example is from native tussock grasslands of the southeastern South Island, which provides habitat for

six skink and one gecko species (Towns et al. 1985; Whitaker et al. 2002; Box 6.1). However, higher diversities are present in some northeastern offshore islands. For example, 13 ha Middle Island (Mercury Islands Group) has three species of gecko and seven species of skink (Towns and Daugherty 1994). These high species diversities are probably possible through the partitioning of environmental resources, but comprehensive niche studies including temporal, spatial and trophic interactions are rare (but see Towns 1975; Towns et al. 1985).

Prior to human arrival, natural densities of lizards were probably very high. For example, at Turakirae Head, Wellington, densities of *W. maculata* populations in the early 1980s were estimated conservatively to be ~4000 per ha (Whitaker 1982), *Toropuku stephensi* at 600 per ha in vinelands on Stephens Island (Hare and Cree 2005) and *O. lineoocellatum* between 1000 and 8000 per ha, depending on location (references within Towns et al. 2002). To facilitate such high densities, often with different species coexisting in finite space, either environmental resources are partitioned or intra- and interspecific competition is very high.

### *6.2.3 Habitat Use and Movement by New Zealand's Lizards*

Studies of lizard communities often categorise lizards by whether they use elevated perches or not, with perches including arboreal and saxicolous (rock dwelling) microhabitats (Vitt et al. 2003). Although we acknowledge that saxicolous habitats may be elevated in some cases (e.g. isolated rock outcrops; tors at Macraes Flat, Otago; Fig. 6.2a), in terms of the New Zealand environment, saxicolous habitats include rock tors, rocky scree, rocky cliffs and/or boulder banks; not all of which are elevated (Fig. 6.2a, b, e). Thus, here we have continued to use the broader classification outlined in Tingley et al. (2013): terrestrial (use the ground, including rocks) and arboreal (use tree/scrub vegetation). In addition, we add semi-fossorial as a category to indicate terrestrial species that primarily use burrows and/or deep leaf litter (Fig. 6.1 d).

In general, New Zealand geckos are classified as arboreal, terrestrial or 'both' (i.e. use both environments while foraging); all *Naultinus* geckos and two *Mokopirirakau* spp. are arboreal (some use refuges on the ground, D van Winkel unpublished data), with the remaining geckos classified as terrestrial (30 %). In contrast, the skinks are generally recorded as terrestrial (92 %; Fig. 6.1d), despite observations of some terrestrial species foraging within scrub and/or trees. For example, the primarily terrestrial *O. fallai* has been observed foraging in trees up to 3 m off the ground (Parrish and Gill 2003), and the saxicolous *O. otagense* is often observed foraging for berries in short scrub (Fig. 6.3c). A more in-depth examination of intra- and interspecific variation in habitat use is warranted, especially for skinks. As additional ecological studies are completed on New Zealand's lizard species, it is likely that revision and reclassification of habitat use categories will be needed.

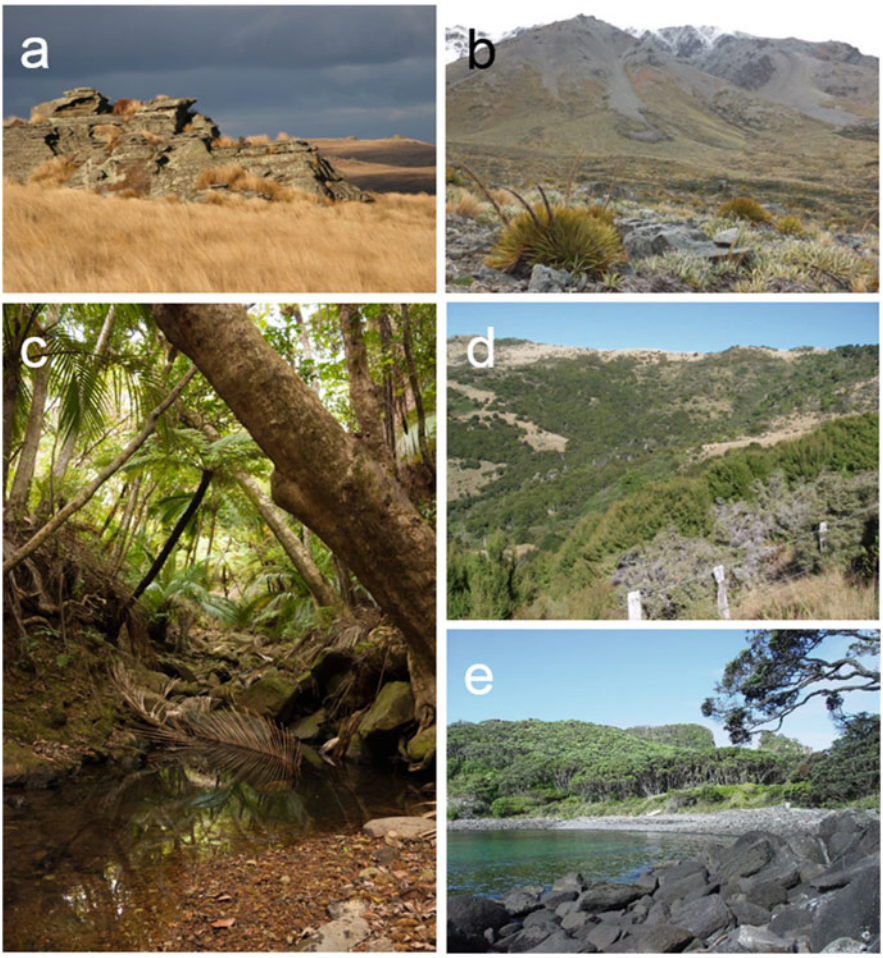



**Fig. 6.2** Examples of habitats used by endemic lizards in New Zealand. (**a**) Modified (periodically burnt for agriculture) tussock grassland at Macraes Flat, Otago (Photo: © Grand and Otago Skink Recovery Programme, New Zealand Department of Conservation). (**b**) Mt Somers Range in alpine/montane area around 1000 m a.s.l (photo: © Marieke Lettink). (**c**) Forest habitat on Great Barrier Island (Photo: © Dylan van Winkel). (**d**) Regenerating shrubland/forest in lowland Banks Peninsula (photo: © Marieke Lettink). (**e**) Coastal forest and boulder beach on Korapuki Island, Mercury Island Group (photo: © David Towns)

Knowledge of microhabitat use, including habitat preferences, movement patterns and the use of retreat sites, provides ecological information helpful in optimising sampling techniques (Lettink and Hare 2016) and accurately evaluating threat status and population trends for conservation (Tingley et al. 2013). Despite the number of lizard species, detailed studies of habitat use by New Zealand lizards are rare, but some excellent examples exist (e.g. Barwick 1959; Towns 1975; Hitchmough 1979; Neilson et al. 2006). This deficit in data is probably due to the

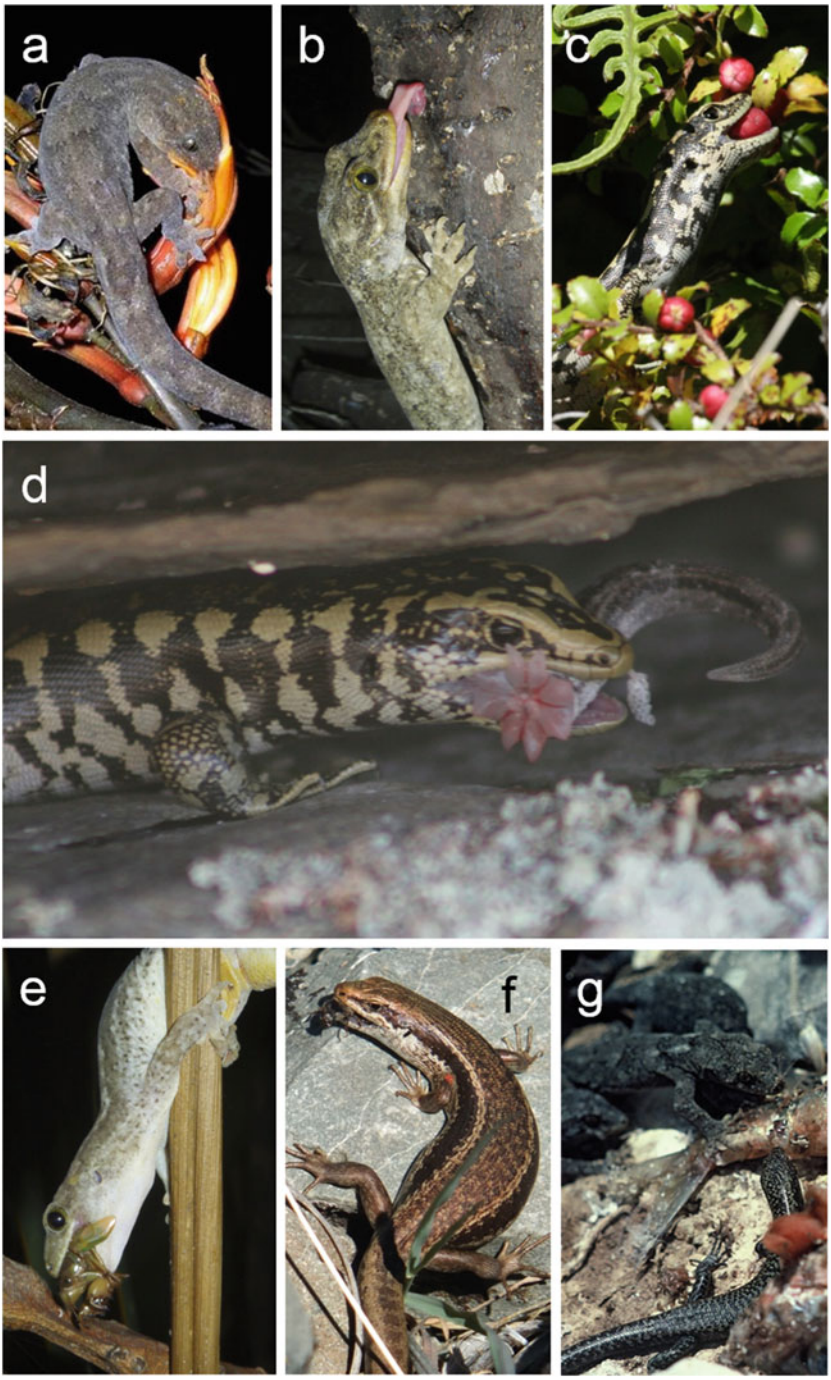



**Fig. 6.3** Diet and foraging behaviour of endemic lizards of New Zealand. (**a**) *Woodworthia maculata* drinking nectar from a flower of *Phormium* sp.; pollen is visible on the back of the head (Photo: © Kelly Hare). (**b**) *Hoplodactylus duvaucelii* licking honeydew oozing from a

long hours of field-work required, coupled with the often cryptic nature and relatively small body size of native lizards (Hare et al. 2007; Cree and Hare 2016). As new techniques and technologies are developed (e.g. lighter and smaller transmitters, camera stations (see Lettink and Hare 2016) and drones), more detailed studies are likely to be possible.

Habitat structure can influence the movement patterns of lizards (McIntyre and Wiens 1999). Familiarity with the landscape may minimise energy expenditure while searching for resources such as food, retreats and mates and reduce time spent in unsuitable habitat, i.e. aid in predator avoidance (e.g. Hoare et al. 2007). Thus, resident animals often move in a predictable manner due to familiarity with their environment (Plummer and Mills 2000). Movement data and dispersal of New Zealand lizards have been recorded through direct observation (*H. duvaucelii*, Whitaker 1968), recaptures of individuals from evenly spaced pitfall traps and/or artificial covers (e.g. *O. whitakeri*, Towns and Elliott 1996; *W.* cf. *brunnea*, Lettink 2007), using telemetry (e.g. *M.* 'Southern forest' Hoare et al. 2013; *O. grande*, Gebauer 2012; *O. otagense*, Eifler and Eifler 1999a) and/or through genetic (e.g. *O. grande*, Berry et al. 2005) and stable isotope studies (*O. suteri*, Janssen et al. 2015). Additionally, populations of a species may vary in their use of habitat. For example, the obligate coastal skink *O. suteri* appears to vary in habitat use depending on their size (e.g. Towns 1975). Since conventional tracking is not possible for *O. suteri* in their boulder beach habitats, Janssen et al. (2015) compared the ratios of isotopes ($^{13}C$:$^{15}N$) of skinks and their prey. Larger skinks (>75 mm SVL) on one island site consumed more terrestrial invertebrates from rank grassland than those <75 mm, which fed mostly on marine species (Janssen et al. 2015). Thus, studies using stable isotopes can add to more conventional habitat-use studies.

Many New Zealand lizards show strong site fidelity, some over extraordinarily long periods of time. Some examples include the following: over an 8-year monitoring study, 92 % of *W. maculata* at Turakirae Head, Wellington, were found within 5 m of previous sightings (Whitaker 1982); one female *H. duvaucelii* from North Brother Island was found within 5 m of its original capture point 29 years later (Thompson et al. 1992); and five of six *O. lineoocellatum* from North Brother Island were within 15 m of their original capture point 5 years later (Hoare et al. 2005). Many other New Zealand lizards have been recorded to have strong

**Fig. 6.3** (continued) Myoporum laetum branch (Photo: © Dylan van Winkel). (**c**) The saxicolous skink, *Oligosoma otagense*, plucking fruit after climbing a *Gaultheria antipoda* shrub (Photo: © Riki Mules). (**d**). *Oligosoma otagense* eating the freshly autotomised tail of the gecko *Woodworthia* 'Otago large'; the skink was seen grabbing the tail of the gecko and later consuming it; the autotomized tail is curled in mid-movement (Photo: © Grand and Otago Skink Recovery Programme, New Zealand Department of Conservation). (**e**) *Woodworthia maculata* eating a cicada (Order Arthropoda; Photo: © Dylan van Winkel). (**f**) *Oligosoma longipes* eating a beetle (Order Arthropoda); orange parasitic mites (*Odontacarus* sp.) are visible in the left axilla (Photo: © Marieke Lettink). (**g**) A skink (*Oligosoma smithi*) and three geckos (*Dactylocnemis* 'Poor Knights') eating regurgitated fish from a seabird (Photo: © Rod Morris/rodmorris.co.nz)

site fidelity; some examples include: *W. chrysosiretica* (Flannagan 2000), *W.* cf. *brunnea* (Lettink 2007), *T. stephensi* (Hare and Cree 2005), *O. whitakeri* (Southey 1985) and *O. grande* (Coddington and Cree 1997).

A revealing study of habitat use was of the large secretive skink *O. homalonotum* on Great Barrier Island. Transmitters on eight adult skinks showed that while tracked they only moved short distances (mean = 2.8 m), remained within 13 m of forested streams and occupied debris dams, burrows in soil, crevices in trees and the crowns of tree ferns and palms (Neilson et al. 2006). However, *O. homalonotum* may move much larger distances, up to 58 m away from streams (Barr 2009). Of note, capture, including attachment of transmitters, can alter the behaviour of animals and may elicit some large-scale movements (e.g. Germano 2005). Additionally, translocated individuals may behave differently from individuals in source populations. For example, movements and range sizes in translocated *H. duvaucelii* are larger than in resident populations (van Winkel 2008), with adult geckos on Tiritiri Matangi Island and Motuora Islands moving up to 34.3 m per day and having range areas up to six times larger (mean = 1524 $m^2$) than resident non-translocated populations. This is compared with *H. duvaucelii* on the Poor Knights Islands, which move up to 25 m per night (Whitaker 1968) and *H. duvaucelii* on Ruamahua-Iti Island which may range over 210 $m^2$ within three nights (Christmas 1995).

Dispersal after translocation is common among animals (Le Gouar et al. 2012) and may be a contributing factor to the historically low success rate of herpetofaunal translocations (Miller et al. 2014). Thus, improving site fidelity of translocated individuals is vital (Germano and Bishop 2008); the technique of penning prior to release may reduce dispersal among translocated individuals, at least in *N. gemmeus* (Knox and Monks 2014). Of interest, some species show strong homing ability, which may also account for some of the large-scale movements recorded post-translocation. For example, over a 9-week period, 54 % of displaced *O. grande* returned to their capture tor, with no difference in homing abilities apparent between age classes and sexes (Stanley 1998). The skinks showed a negative correlation between homing ability, time to home and distance moved, and no individuals homed when moved >100 m (Stanley 1998). Similarly, some *W. maculata* have been observed to return at least 110 m to their capture location over 32 days (Marshall 1983). However, some species show no apparent homing ability (e.g. *W.* cf. *brunnea*; Lettink 2007).

## 6.3 Diet, Seed Dispersal and Pollination

Animals tend to exploit food resources that offer maximum nutritional or energetic returns relative to time spent foraging (Pyke et al. 1977). Dietary components have been determined by direct observation of individuals, through stomach or scat analyses (e.g. Barwick 1959; Towns 1975), or through stable isotope analyses; the latter of which may be more reflective of diet over long periods (e.g. Janssen et al. 2015). Dietary components have been reported for 40 species of lizards (38 %)

in New Zealand, and most appear to be omnivorous. The main items recorded in the diet of skinks and geckos are arthropods (e.g. Table 6.1), but other organisms are often consumed, including smaller lizards or autotomized tails and carrion of larger vertebrates (Table 6.1). However, no 'other invertebrates' (e.g. molluscs and worms) have yet been recorded in the diet of geckos (Table 6.1). Many lizard species feed on coastal invertebrates and carrion (e.g. Fig. 6.3 g) and must cope with the physiological challenges of high salt content in their food. One species, *O. suteri*, overcomes this problem by secreting sodium (Na) from nasal salt glands (Janssen et al. 2015). Whether other species found near the coast are similarly adapted to salty diets is unknown. Some New Zealand lizards (~60 %) also readily eat sugar sources of fruit, honeydew and nectar (Evans et al. 2015; Wotton et al. 2016; Fig. 6.3a, b, c) and other plant matter (Table 6.1). Consumption of 'other' plant matter is often assumed to be accidental ingestion during prey capture (e.g. Freeman 1997). However, *O. grande* have been observed systematically plucking and consuming the bright yellow petals of *Hieracium* spp. flowers (Tocher 1998); prior to this observation, petals were assumed to be consumed accidentally.

Internationally, lizard-plant interactions are regarded as rare and less important than bird-plant and insect-plant interactions for both the ecology and evolution of plants (Olesen and Valido 2003, 2004). However, evidence from New Zealand studies suggests that lizards are, or once were, important components of plant reproductive strategies (e.g. Whitaker 1987; Towns and Daugherty 1994; Wotton et al. 2016). To date, the fruits of 23 native plant species have been recorded as being consumed by New Zealand's lizards, with greater numbers of white–blue fruits eaten than red fruits (see Wotton et al. 2016 for review). Additionally, lizards can disperse seeds, which later germinate up to around 20 m from the parent plant, allowing seeds to disperse to safe establishment sites (Wotton et al. 2016). Thus, lizards are important seed dispersers, even at reduced densities on the mainland, and in areas lacking frugivorous birds may be the only dispersers present (Whitaker 1987; Wotton et al. 2016).

Lizards can also be effective pollinators (Traveset and Sáez 1997; NyHagen et al. 2001), and one of the earliest suggestions that lizards are pollinators was based on observations on New Zealand geckos (Whitaker 1987). In one study over two-thirds of geckos (*Dactylocnemis* 'Poor Knights') visiting flowers were observed to carry pollen, with pollen being carried up to at least 50 m from the source plants and for at least 12 h, providing opportunity for cross-pollination (Whitaker 1987). The reported density of gecko visitors on flowers in New Zealand is between 5 and 8 geckos per $m^2$ (Whitaker 1968, 1987), with up to five geckos observed feeding together on a single inflorescence (Whitaker 1987). Lizard densities reported on flowers in New Zealand are around three times greater than reported in international studies (Eifler 1995). However, coevolution of lizards and plants appears unlikely as, to date, no plants have been recorded as being peculiarly adapted for pollination by lizards (Whitaker 1987); additionally, some studies suggest that lizards play a minor role in the New Zealand pollinator systems (Newstrom and Robertson 2005).

**Table 6.1** Items recorded in the diet of New Zealand lizards in the wild

| Species | Plant matter | | | | Chordates | | | | Arthropods | | | | | | Other invertebrates | | | | Sources |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fruit | Honeydew | Nectar | Other | Bird | Fish | Mammal | Reptile | Arachnida | Chilopoda | Diplopoda | Entognatha | Insecta | Malacostraca | Annelida | Mollusca | Nemotoda | Platyhelminthes | |
| Skinks | | | | | | | | | | | | | | | | | | | |
| *Oligosoma acrinasum* | | | | | | | | | ● | | ● | | ● | ● | | ● | | | Thomas (1985) |
| [a]*Oligosoma aeneum* | ◊ | | | | | | | ● | ● | | | | ● | ● | ● | ● | ● | | McCann (1955), Porter (1987), and Barwick (1959) |
| *Oligosoma alani* | ● | | | | | ● | | ● | ● | ● | ● | ● | ● | ● | | ● | | | Southey (1985) |
| *Oligosoma fallai* | ● | | | ● | ● | ● | | | ● | ◊ | ◊ | ◊ | ● | ● | | | | | Parrish and Gill (2003), Whitaker (1968), and McCann (1955) |
| *Oligosoma grande* | ● | | | ● | | | | | ● | | | | ● | | | | | | Tocher (2003), Eifler and Eifler (1999a,b), and Tocher (1998); Fig. 6.3b |
| *Oligosoma homalonotum* | | | | | | | | | ● | | | | ● | | | ● | | | Towns et al. (2002) |
| *Oligosoma inconspicuum* | ● | | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | Patterson (1985) |
| *Oligosoma infrapunctatum* | ● | | | | | | | | | | | | ● | | | | | | Efford et al. (1997) and Duncan (1999) |
| *Oligosoma lineoocellatum* | ● | | ● | | | | | ● | ● | | ● | | ● | ● | ● | ● | | | Spencer et al. (1998), Towns et al. (2002), Robb (1980), and Phillpot (2000) |
| *Oligosoma longipes* | | | | | | | | | | | | | ● | | | | | | Figure 6.3f |
| [a]*Oligosoma maccanni* | ● | | | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | Freeman (1997), Patterson (1985, 1992) |
| *Oligosoma macgregori* | | | | | | | | | ◊ | ◊ | ◊ | | ● | ◊ | | | | | Robb (1980) |

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oligosoma moco* | ● | | ● | | | | | | ◊ | ◊ | ◊ | ◊ | ● | ◊ | | | | | Whitaker (1968), Wotton et al. (2016), Patterson (1992), and Stephenson (2012a) |
| *Oligosoma nigriplantare* | | | | | | ● | | | ◊ | ◊ | ◊ | ◊ | ● | ◊ | | | | | Fleming (1939) and Robb (1980) |
| *Oligosoma oliveri* | ● | | | | ● | ● | | | ● | ● | ● | | | ● | | ● | | | Southey (1985) |
| *Oligosoma ornatum* | | | | ● | | | | | ● | | | | ● | ● | ● | ● | | | Porter (1987) |
| *Oligosoma otagense* | ● | | | | | | | ● | ● | | | | ● | | | | | | Tocher (2003); Fig. 6.3c |
| [a]*Oligosoma polychroma* | ● | | | | | | | | ● | | | | ● | ● | ● | ● | ● | | Gill (1976) and Barwick (1959) |
| [a]*Oligosoma* aff. *polychroma* Clade 5 | ● | | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | Patterson (1985) and Freeman (1997) |
| *Oligosoma smithi* | ● | | | | ● | ● | | | ◊ | ◊ | ◊ | ◊ | ● | ◊ | | | | | Towns (1972), Whitaker (1968) and Towns et al. (2002); Fig. 6.3 g |
| *Oligosoma striatum* | | | | | | | | | | | | | ○ | | | | | | Melgren (1980) |
| *Oligosoma suteri* | | | | | | ● | ● | ● | | | | | ● | ● | | ● | | | Towns (1975); Parrish and Gill (2003) and Stephenson (2012b) |
| *Oligosoma whitakeri* | ● | | | | | | | | ● | ● | ● | | | ● | | ● | | | Southey (1985) |
| *Oligosoma waimatense* | ● | | | ● | | | | ● | ◊ | ◊ | ◊ | ◊ | ◊ | ◊ | | | | | Whitaker (1985) and Patterson (1997) |
| *Oligosoma zelandicum* | | | | | | | | ● | ● | | | ● | ● | ● | | ● | | | Gill (1976) |

(continued)

**Table 6.1** (continued)

| Species | Plant matter | | | | Chordates | | | | Arthropods | | | | | | Other invertebrates | | | | Sources |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fruit | Honeydew | Nectar | Other | Bird | Fish | Mammal | Reptile | Arachnida | Chilopoda | Diplopoda | Entognatha | Insecta | Malacostraca | Annelida | Mollusca | Nemotoda | Platyhelminthes | |
| Geckos | | | | | | | | | | | | | | | | | | | |
| *Dactylocnemis pacificus* | ● | | ● | | | | | | | | | | ● | | | | | | Robb (1980) |
| [a]*Dactylocnemis* 'Poor Knights' | ● | | ● | | | ● | | | | | | | ● | | | | | | Wotton et al. (2016) and Whitaker (1968); Fig. 6.3 g |
| *Hoplodactylus duvaucelii* | ● | ● | ● | ● | ● | | | ● | ● | | | | ● | | | | | | Whitaker (1968), Barwick (1982) and Harper (1983); Fig. 6.3b |
| *Mokopirirakau* 'Southern forest' | | | | | | | | | | | | | ● | | | | | | Hoare et al. (2013) |
| *Naultinus elegans* | | | | | | | | | | | | | ● | | | | | | Robb (1980) |
| *Naultinus grayii* | ● | | | | | | | | | | | | ● | | | | | | Hitchmough (1982) and Wotton et al. (2016) |
| *Naultinus manukanus* | | | | | | | | | ◊ | ◊ | ◊ | ◊ | ○ | ◊ | | | | | Robb (1980) |
| *Naultinus stellatus* | ○ | | | | | | | | | | | | ● | | | | | | Conway and Gaynor (1979) and Robb (1980) |
| *Naultinus tuberculatus* | | | | | | | | | | | | | ● | | | | | | Robb (1980) |
| *Toropuku stephensi* | ● | | | | | | | | | | | | | | | | | | Wotton et al. (2016) |
| *Tukutuku rakiurae* | | | | | | | | | ○ | | | | ○ | ○ | | | | | Thomas (1981) |
| [a]*Woodworthia* cf. *brunnea* | ● | | | | | | | | | | | | | | | | | | Freeman (1994) |

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Woodworthia chrysosiretica* | | | | | | | | | ● | | | | ● | | | | | | Robb (1980) |
| *Woodworthia maculata* | ● | ● | ● | | | | | | ● | | | | ● | | | | | | Evans et al. (2015) and Whitaker (1982); Fig. 6.3a |
| *Woodworthia* 'Southern Alps' | ● | | | | | | | | | | | | | | | | | | Wotton et al. (2016) |

Data were selected from published sources, theses and reports (in that order, with citations with the most data selected first; i.e. not all citations are listed). Dietary item included as: *filled circle* = lizard directly observed eating item and/or item found in stomach contents and/or in faeces; *unfilled circle* = reported as in diet, but specific item not reported; *diamond* = inferred as in diet. Other plant matter refers to leaves and petals. Birds include carcasses and/or broken eggs. Reptiles may include only the consumption of tails. Fish is either regurgitated from birds and/or carcasses. Mammals refer to consumption of carcasses

[a]Species has been inferred from its geographic location coupled with taxonomy outlined in Hitchmough et al. (2016a)

Reported consumption of sugar sources by skinks is mainly for fruit, with only two skinks recorded as drinking nectar (*O. lineoocellatum* and *O. moco*; Towns et al. 2002; Stephenson 2012a), and none reported to consume honeydew. However, geckos are avid drinkers of nectar. An experiment whereby the volume of nectar (53 % [sugar]) was increased artificially by 40–100 % not only increased the number of geckos visiting flowers, but geckos appeared to select stalks with more male flowers (Eifler 1995); male flowers have higher rates of nectar secretion and higher sugar concentrations than female flowers. Similarly, numbers of geckos increased exponentially as numbers of inflorescences increased indicating that gecko distribution reflects nectar availability (Eifler 1995). However, long-term studies indicate that the diet of New Zealand's lizards probably fluctuates throughout the year, changing opportunistically with season and environmental temperature (e.g. Whitaker 1982; Tocher 2003).

Few studies indicate the sizes of prey items, but those that do tend to show the expected trend for the size of prey consumed to be proportional to the size of the species (e.g. Hitchmough 1979; Whitaker 1982); smaller species tend to eat smaller-sized items. However, lizards will attempt to eat large items too, which can be to their detriment. For example, a skink (*O. oliveri*) was observed choked to death on a scavenged piece of fish (Whitaker 1968). Finally, trends in diet are not always straightforward. For example, some species show sex-biased difference in some studies, but not others, although this may be related to seasonal differences in food availability. For example, in March *O. grande* males tend to attempt to catch large strong-flying insects, and males use a salutatory search pattern (where individuals alternatively move and pause while foraging; Eifler and Eifler 1999b), whereas females eat more frequently and spent more time eating. However, a later study showed no difference in diet among sites, ages classes and sexes, but showed an increase in fruits eaten in May (53 %) compared with November (20 %; Tocher 2003). Thus, food intake and dietary diversity varies considerably among the seasons. Of interest, some species have been recorded eating items that are presumably not present during their purported activity phase. For example, in one study *O. lineoocellatum* consumed more nocturnal (53 %) than diurnal prey items (32 %; Spencer et al. 1998), which suggests either incorrect apportioning of activity period to prey items, or activity at night by these diurnally foraging skinks.

## 6.4 Activity and Behaviour

### *6.4.1 Classification and Measurement of Activity Phase of Geckos and Skinks*

Squamates are ancestrally diurnal ectotherms, and diurnal activity is more likely to enable them to reach body temperatures necessary for activity and physiological functions (Hare and Cree 2016). Among squamates, only the ancestor of geckos and

Autarchoglossa (skinks, anguimorphs, snakes and relatives) has evolved nocturnality (Vitt et al. 2003). The use of time (temporal niche) varies among lizard species; historically, species have been classified as either diurnal (day active), nocturnal (night active) or crepuscular (active dawn and dusk). More recent studies include a 'both' (nocturnal and diurnal) or 'nocturnally foraging' classification (Pianka and Vitt 2003; Gibson et al. 2015), as a way to show that many lizard species are not constrained by our classifications of activity; and this variability appears to be especially true for New Zealand's lizards. For example, of the 33 nocturnally foraging geckos, 64 % have been observed emerged and basking during the day (e.g. Fig. 6.4b) although no diurnally foraging geckos (all *Naultinus*) have yet been observed active at night (Fig. 6.1e). For the skinks, activity patterns are less well defined. Within the nine species of nocturnally foraging skinks around half have also been observed foraging by day and/or at dawn and dusk (Fig. 6.1f; *O. oliveri*, *O. ornatum*, *O. macgregori*, *O. suteri* and *O. whitakeri*; Robb 1980; Porter 1987; Towns 1999), and one (*O. fallai*) has been reported as both strongly active during the day and night (Parrish and Gill 2003). Additionally, some diurnal skinks have been observed foraging at night (e.g. captive *O. striatum*; Whitaker 1998). Interestingly, all nocturnally foraging skinks and recorded cases of nocturnal activity in skinks have been reported in species and populations from the North Island, most on low-lying offshore northern islands (Towns 1999). There appears to be no geographic variation in activity patterns for the geckos, as seen in the skinks (KM Hare unpublished data). Whether altitude influences activity patterns among New Zealand's lizard species has not been investigated, nor have patterns over over winter.

With these daily activity patterns in mind, it is not surprising that, when compared with review data for activity of lizards worldwide (Vitt et al. 2003), New Zealand's endemic lizards do not adhere to general trends. For example, globally ~62 % of geckos are classed as nocturnal, ~36 % as diurnal and ~2 % as 'both'. Currently, New Zealand geckos have only 28 % recorded as nocturnal foragers, 21 % as diurnal foragers and 49 % as primarily nocturnal foragers that have been recorded out by day (e.g. basking, Hare and Cree 2016; Fig. 6.1e). Similarly, globally ~2 % of Autarchoglossa are classified as nocturnal, ~97 % as diurnal and 1 % as both nocturnal and diurnal, whereas 7 % of New Zealand's skinks are currently classified as nocturnally foraging, 8 % are nocturnally foraging with some diurnal behaviour, 77 % are diurnally foraging and 3 % are crepuscular, but also seen by day (Fig. 6.1f).

One way to determine the activity phase of lizards is by recording a time series. For example, a time series for *H. duvaucelli* from the Poor Knights Islands was developed from over 150 h of field observation from November to January across two seasons (Whitaker 1968). Whitaker (1968) observed that the geckos emerged at dusk, activity increased rapidly up till 2100 h, continuing until ~0330 h, after which the geckos began to seek retreats, with all in retreats by 0430 h. By day, the geckos retreated under stones, logs, bark and into rock crevices, hollow trees and petrel burrows. However, geckos were observed to bask in the sunlight where it fell near a retreat. Although mostly terrestrial in behaviour, they were sometimes

predominantly arboreal where another species, such as *O. oliveri*, was present in high numbers. From these data, *H. duvaucelli* can be classified as a nocturnal forager with some diurnal emergence, with changes in habitat use with the presence of predators (see Sect. 6.5). As more data are collected on the lizards of New Zealand, their activity periods may be found to differ from those currently assigned, either as a species or as populations (e.g. with environmental temperature, latitude, altitude and/or the presence of certain predators and/or food sources).

### *6.4.2 Sociality, Courtship, Mating and Possible Parental Care*

In lizards, sociality is generally agreed to be uncommon (Gardner et al. 2016), and parental care is even less commonly reported (Somma 2003). Some New Zealand lizards show social tendencies, although genetic studies are needed to confirm relatedness of individuals. For example, *O. otagense* are often seen in male–female pairs (Coddington and Cree 1997) and potentially family groups (Fig. 6.4c). Additionally, adult *W. maculata* have been observed assisting juveniles, suggesting possible social assistance and/or parental care (Hoare and Nelson 2006). Similarly, ~42 % of observed captive-held *O. maccanni* that have just given birth will bite open placental membranes that may enclose offspring at birth (Chamberlain et al. 2010), suggesting a rudimentary form of parental care.

Aggregative behaviour (where two or more conspecifics have concurrently overlapping home ranges) is another form of sociality and in squamates is generally formed to avoid predators, where insufficient retreats are present and/or as a way to control heat or water flux (Brattstrom 1974; Shah et al. 2003). To date, only 94 of ~9905 squamate species have been recorded as forming an aggregation (Gardner et al. 2016; Uetz and Hosek 2016). Aggregations of communally basking *O. acrinasum* have been observed in coastal Fiordland, with up to 12 skinks of all sizes intertwined in piles, suggesting potential thermal benefits (Thomas 1985). In contrast, some nocturnally foraging diplodactylid geckos form diurnal aggregations that consist of male–female pairs (sometimes with juveniles), or a mix of adults and juveniles (Fig. 6.3d; e.g. Hare and Hoare 2005; Barry et al. 2014). These gecko aggregations have been reported to include up to 200 individuals (Bauer 1990) and are formed in environments that appear to have many retreat sites available. Occurrence of aggregations despite the presence of multiple (apparently) suitable retreat sites implies a complex social system and/or other benefits (Shah et al. 2003; Hare and Hoare 2005; Barry et al. 2014). Of interest, no *H. duvaucelii* aggregations contain multiple males, and males with multiple females are larger than males forming single male:female pairs. This suggests that in *H. duvaucelii*, if sex-specific grouping patterns are related to mating, then larger males might be guarding females, and excluding smaller males, thereby potentially gaining mating advantages (Barry et al. 2014). However, the high variance in adult sex ratios within

aggregations among different diplodactylid species (e.g. Hare and Hoare 2005) suggests that aggregations may not always represent family groups and/or harems. Additionally, no *Naultinus* geckos have been observed forming aggregations in the wild. Aggregation may be widespread and frequent in the diplodactylid geckos of New Zealand, but its taxonomic distribution, and purpose, needs clarification.

Courtship is generally a stereotypical sequence of behaviours that leads to mating. Although courtship behaviour is well studied in many vertebrates (e.g. birds), including many lizards overseas (Jenssen 1977), little is known about the courtship behaviour of New Zealand lizards. The most in-depth description for courtship behaviour for the gecko *W*. cf. *brunnea*, for which a list of eight stereotypical behaviours were identified: (1) Male approaches female jerkily or hesitantly; (2) Female approaches male jerkily or hesitantly; (3) Male trembles/shakes his head or body at the female; (4) Female trembles/shakes her head or body at the male; (5) Male sits on female's back and holds or nibbles her; (6) Male sits on female's back and bites her firmly in the flank or back of the neck; (7) One individual licks the other's cloaca. (8) Male on female's back with tails entwined/mating (Todd 2005).

In this species, larger males generally courted females more often, and males were observed courting up to four different females on the same day, suggesting that the mating system for this species is polygynandrous (Todd 2005).

For skinks, copulatory behaviour has been recorded only in wild *O*. *smithi*, where Whitaker (1968) wrote the following:

> two lizards were [observed] circling each other when first noticed. The male then approached the female, seized the side of her neck in his jaws, and thrust the lower part of his body under her tail so that their vents were pressed together [. . .]. After a few seconds the female wriggled free and scuttled off into the scrub, followed moments later by the male. (Whitaker 1968)

Perhaps New Zealand skinks follow a stereotypical sequence of courtship behaviours, but an ethogram has yet to be developed for any species of *Oligosoma*. Copulation position for skinks has been illustrated in captive *Oligosoma* (as [*Leiolopisma zelandica*]), with the male appearing to insert a hemipene from one side of the tail (Barwick 1959). This position has also been observed in *O*. *grande* (see Fig. 6.3a). Male squamates from elsewhere in the world often show a preference for using the right or left hemipene, and this may be true for New Zealand skinks and geckos, but requires further observations to confirm (Shine et al. 2000).

The mating system of most *Oligosoma* skinks is unknown. The most in-depth studies are for populations of *O*. *grande* at Macraes Flat, Otago. Observations of mating suggested a polygynous mating system, with males visiting several females sequentially (Eifler and Eifler 1999a). However, genetic studies showed that *O*. *grande* is in fact promiscuous, with approximately half of females and three quarters of males having more than one partner in a breeding season (Berry 2005). Additionally, around 18 % of offspring resulted from mating of related individuals, and related adults were often present on the same rock tor; proportions of related


**Fig. 6.4** Some behaviours of endemic lizards of New Zealand. (**a**) Copulation of *Oligosoma grande*; the male is biting the side of the female, with his tail curled under and inseminating her presumably via his left hemipene (Photo: © James Reardon). (**b**) The nocturnally foraging gecko *Woodworthia* 'Otago large' basking by day at the entrance to a rock crevice (Photo: © Riki Mules). (**c**) Aggregation of five basking *Oligosoma otagense*, including two adults and three juveniles (Photo: © James Reardon). (**d**) Large aggregation of *Woodworthia maculata* within a bird nesting box; included are males, females and juveniles (Photo: © Dylan van Winkel)

individuals inhabiting the same rock tor did not differ between modified (agricultural) and native tussock grasslands (Berry 2005). Despite some antagonistic interactions among the adults, young lizards (<1 year) commonly shared crevices and maintained physical contact with adults without eliciting any obvious antagonistic response from adults (Eifler and Eifler 1999a).

### *6.4.3 Aggression and Competition*

Typically, aggressive encounters within species are stereotypical to reduce the possibility of damage and death. Among skinks, aggressive encounters often begin by way of a slow vibration of the tail tip (e.g. Torr and Shine 1994). A typical combat sequence has been recorded in captive *O. suteri* (Towns 1975) and involves: (1) opponents sight each other, and Male-A (lower ranked) begins to vibrate his tail; (2) Male-B (higher ranked) bites vibrating tail at tail base; (3) Male-A bites neck of Male-B causing him to release tail base; (4) Male-A then flees with his tail still vibrating and Male-B in pursuit (Towns 1975). *Oligosoma* skinks have

been observed undergoing aggressive encounters during the breeding season and over finite resources (e.g. Eifler and Eifler 1999a), although there appears to be a spectrum of aggression among skinks. At one end are the apparently social skinks (see Sect. 6.4.1), moving through the more territorial species, such as *O. inconspicuum* (often scarred from aggressive encounters which include mainly chasing and biting behaviours, although other behaviours included head butting and tail lashing; Patterson 1992), through to those species that are difficult to keep in captivity due to individuals killing each other during aggressive encounters (e.g. *O. macgregori*; Newman 1994).

Competition is where the interaction between organisms or species results in reduced biological fitness of one when the other is present; limited supply of a resource (e.g. food, water and territory) is seen as a key factor (Downes and Bauwens 2001). Thus, competition among and within species is often inferred by niche separation (discussed earlier in Sect. 6.2). For example, although some *H. duvaucelii* populations tolerate retreat sharing with other species (Whitaker 1968), competition among species for access to sugar sources on Korapuki Island, Mercury Island group, influences their habitat use (Evans et al. 2015). In particular, *W. maculata* avoid trees with high populations of the larger gecko *H. duvaucellii* (Evans et al. 2015), and juvenile *W. maculata* avoid sugar sources used by larger adults, indicating competition between different age classes within a species (Evans et al. 2015). Whether these patterns are related to competition per se (biological fitness) and/or potential predator avoidance (see Sect. 6.5 for more discussion) is unclear and warrants further investigation. Competition with introduced pests has also been reported (e.g. European wasps (*Vespula germanica*) drink honeydew Nelson et al. 2016 for review of this topic).

## 6.5 Defence and Predators

### *6.5.1 Defence Tactics of New Zealand's Lizards*

Most animals undergo fight or flight responses in response to danger. In response to humans (a predator of native lizards; Natusch 1979), *Naultinus* geckos may freeze, using crypsis as camouflage, and, if approached, may drop to the ground to flee (Hitchmough 1979). If cornered, some *Naultinus* may elevate their posture, arching their backs and standing on toes, opening their mouths in a wide gape to show the brightly coloured inside (Box 6.2; Woodward 1941). When handled, both skinks and geckos will generally writhe and frequently bite (e.g. *O. oliveri* and *H. duvaucelii*, Whitaker 1968). Some species of skinks and geckos make vocalisations during handling (e.g. *O. homalonoton*, Towns and McFadden 1993), and some geckos and skinks have been heard vocalising within their retreats (Box 6.2). Flight responses generally include dashing to the nearest retreat, and for some skinks and geckos that live near the water, this may be into the water itself

## Box 6.2 Vocalisations & threat display

Several species of New Zealand's lizards vocalise. For example, the skink *Oligosoma homalonotum* 'squeaks' when disturbed or handled (the latter often accompanied by mouth gapes and biting; Towns & McFadden 1993), and *O. acrinasum* 'squeak' while evading capture and during refuge sharing (Thomas 1985). However, the geckos have more vocal ability, which is unsurprising considering that vocalisations are well documented in geckos overseas (e.g. Werner 1973). The vocal repertoire of New Zealand's geckos range from faint chirps and squeaks to loud croaks and barks (McCann 1955; Whitaker 1982). These vocalisations are classified as 'distress' or 'social' calls.

Defence posture of *Naultinus punctatus* showing the bright blue inside of the mouth (Photo: © James Reardon)

Distress calls probably evolved to delay a predatory attempt and/or to surprise a predator into relaxing its grasp, both enabling escape. Distress calls can be very loud, some heard up to 10 m away (e.g., Hitchmough 1979), and are recorded in many species of *Naultinus*. Two types of distress call have been recorded: (i) a short-duration single burst of frequency ~4,500 – 5,000 hz; (ii) a fast series of regularly spaced short chirps (Hitchmough 1979). The former is often associated with defensive posturing, whereby the inflated body is raised high, the throat distended and the mouth opened wide to reveal the often brightly coloured interior (see picture above right). Defensive elevated posturing is often accompanied by vigorous tail movements, aggressive lunges and loud vocalisations (Woodward 1941). At lower environmental temperatures often less stimulus is needed to evoke the defensive call and posture (Whitaker 1970).

A range of other vocalisations have been reported in geckos, some of which appear to be social in nature. For example, after a male *Woodworthia* 'Otago Large' was introduced to a cage of several females, chattering was heard a few minutes later (Alison Cree pers. comm). Finally, analysis of the voice indicates that the genera *Naultinus* and *Mokopirirakau* can be 'easily separated' (Whitaker 1982), suggesting species-specific repertoires.

To hear vocalisation of *Naultinus rudis* visit:
https://www.youtube.com/watch?v=kF720e7zW0k

**Box 6.2** Vocalisations and threat display

(see Hare and Miller 2009 for review). Species may also change their behaviour and habitat use in the presence of predators and/or competitors. For example, *H. duvaucelli* use different microhabitats in the presence of *Rattus exulans* (Hoare et al. 2007).

When evasion and escape fail to deter threats, lizards use their major (final) defence mechanism, which is caudal autotomy; involving breaking and discarding the tail at predetermined fracture planes. However, autotomy can occur during aggressive intraspecific encounters, and some lizard species shed their tail without direct contact with a predator (Arnold 1984). Thus, care should be taken when using prevalence of previous tail loss as an indicator of predatory interactions. Autotomy may enable the lizard to flee and also provides a spontaneously moving distraction (Arnold 1988). The benefit of caudal autotomy is thus immediate survival, and over time lizards can regenerate their tails. However, autotomy also induces physiological and functional costs, including reduced: reproductive output, growth rate, locomotor performance, social status, mating opportunities and probability of future survival (see Hare and Miller 2010 and references within). Thus, lizards will exhibit crypsis, escape and an aggressive response prior to resorting to tail autotomy (Arnold 1988). Reported tail loss in the field can be high. For example, 95 % of *O. fallai*, 90 % of *O. ornatum* and 92 % of *D.* 'Three Kings', on the Three Kings Islands had regenerating tails (Parrish and Gill 2003). Tail autotomy appears to be lower in arboreal species such as *Naultinus* geckos (e.g. tail loss of *N. manukanus* from Stephens Island ranged from 10 to 14 % of the sampled population; Hare et al. 2007). However, whether these patterns of tail loss with microhabitat use are ubiquitous requires further investigation. In some New Zealand lizards, predation pressure and/or social interactions, rather than innate disposition, probably influences the field rates of tail loss (Hare and Miller 2010).

### *6.5.2 Predators of New Zealand's Lizards*

Lizards are a key component in the diet of many predatory species, and 50 species have been reported as predators of New Zealand's lizards, including five invertebrates (Table 6.2). Internationally, birds are considered the most frequent predator of reptiles (Martín and López 1996). In New Zealand, birds comprise 51 % of species reported to prey on lizards (18 native and seven introduced bird species; Table 6.2). However, the intensity of predation among species varies, with some birds specialising in hunting lizards at certain times of the year. For example, the sacred kingfisher (*Todiramphus sanctus*) is an avid predator of lizards, especially during the breeding season (see Nelson et al. 2016 for details). Lizards are also a key component of New Zealand's fauna (see Towns et al. 2016), and six species of New Zealand's lizards have been recorded to prey upon other lizard species in the wild, often only consuming the autotomized tail (see Sect. 6.3; Fig. 6.3d; Table 6.1, 6.2). However, in New Zealand, predation by introduced mammals is of greater conservation concern (see Towns et al. 2016 and Nelson et al. 2016 for more

discussion). Evidence of detrimental impacts by mammals includes: (1) greater species diversity and population density of lizards on mammal-free islands than unmanaged mainland sites; (2) where mammals are exterminated from islands, or reduced to very low numbers on the mainland, positive responses such as increase in the range of habitats occupied, population densities and reproductive success of lizards is observed (Towns and Daugherty 1994; Towns 1996; Reardon et al. 2012).

Almost all introduced mammalian predators are reported as preying upon lizards (Table 6.2), with high rates of lizard consumption reported in some mammals. For example, the stomach contents of a cat (*Felis catus*) from Macraes Flat, Otago, held 14 lizards from one morning's hunting effort, including threatened species (Daugherty and Towns 1991). This report is not a one-off event, or even the maximum number recorded. Predation by cats was first described in 1870, where 36 lizards were found in the stomach of a feral cat (Taylor 1870). Mice (*Mus musculus*) have been observed directly attacking lizards (Newman 1994) and with lizards in stomach contents (Wedding 2007). However, stomach contents and faeces used for analyses of dietary components only reveal recent intake, whereas stable isotopes and/or DNA analyses can provide a less biased cumulative account of consumption (e.g. Janssen et al. 2015). Although the common brushtail possum (*Trichosurus vulpecula*) is reported to prey upon vertebrates such as birds (e.g. Brown et al. 1993), we found no published evidence of their predation on lizards. Non-predatory mammals may also impact lizard abundance and survival. For example, intense grazing by European rabbits (*Oryctolagus cuniculus*) reduces shelter and food availability for lizards (Norbury 2001), and control of rabbits without control of predatory mammals also results in predators switching to prey more heavily on skinks (Norbury 2001).

Introduced amphibians and invertebrates also prey upon New Zealand's lizards (Table 6.2), including European wasps (Nelson et al. 2016; Table 6.2). In unnatural situations (e.g. captivity and field traps), species that may not normally be capable of capturing lizards can become predators. For example, endemic crabs (*Leptograpsus variegatus*) have been observed killing and consuming lizards trapped within pitfall traps (D. Towns unpub. data). Of interest is a report of a lizard in the stomach of a caught marine fish (Anonymous 2003), which suggests the lizard may have been in the water either hunting for prey (e.g. Whitaker 1968), seeking refuge from predators (e.g. Hare and Miller 2009), accidently after being washed off rocks or actively dispersing. Finally, sex-biased predation pressure may exist. For example, more pregnant female *O. maccanni*, than males, were recorded in the diet of cats (Middlemiss 1995). Pregnant or gravid female lizards may be most at risk from behaviours such as avid sun basking, and also their changed shape and reduced locomotor capacity (Hare and Cree 2016), but this needs further investigation.

**Table 6.2** Organisms recorded as preying upon endemic lizards of New Zealand in the wild

| Description | Order | Species | Skinks | Geckos | Source (examples only) |
|---|---|---|---|---|---|
| Native birds | Accipitriformes | Swamp harrier (*Circus approximans*) | ● | ● | Pierce and Maloney (1989) and Whitaker (1972) |
| | Charadriiformes | Black-fronted tern (*Chlidonias albostriatus*) | ● | | O'Donnell and Hoare (2009) |
| | Charadriiformes | Red-billed gull (*Larus novaehollandiae*) | □ | □ | Oliver (1955) |
| | Coraciiformes | Sacred kingfisher (*Todiramphus sanctus*) | ● | ● | Fitzgerald et al. (1986) |
| | Cuculiformes | Long-tailed cuckoo (*Eudynamys taitensis*) | ● | | Falla et al. (1966) |
| | Gruiformes | Banded rail (*Gallirallus philippensis*) | ● | | Stephenson et al. (1966) |
| | Gruiformes | Pukeko (*Porphyrio melanotus*) | ◊ | ◊ | Muggeridge and Cottier (1931) and Carroll (1966) |
| | Gruiformes | Takahe (*Porphyrio hochstetteri*) | ● | ● | Whitaker (1991) |
| | Gruiformes | Weka (*Gallirallus australis*) | ◊ | ● | Potts (1871), Coleman et al. (1983) and Thomas (1982) |
| | Laridae | Southern black-backed gull (*Larus dominicanus*) | □ | □ | Oliver (1955) |
| | Falconiformes | New Zealand falcon (*Falco novaeseelandiae*) | ● | ● | Fox (1977) |
| | Passeriformes | New Zealand pipit (*Anthus novaeseelandiae*) | ◊ | ◊ | Wilkinson and Wilkinson (1952) |
| | Passeriformes | North Island fernbird (*Bowdleria punctata*) | ● | | Ball and Parrish (2005) |

(continued)

**Table 6.2** (continued)

| Description | Order | Species | Skinks | Geckos | Source (examples only) |
|---|---|---|---|---|---|
| | Pelecaniformes | Australasian bittern (*Botaurus poiciloptilus*) | □ | □ | Buddle (1951) |
| | Pelecaniformes | White-faced heron (*Egretta novaehollandiae*) | ● | | Pierce (1980) |
| | Psittaciformes | Kakapo (*Strigops habroptilus*) | ◊ | ◊ | von Hugel (1875) |
| | Strigiformes | *Laughing owl (*Sceloglaux albifacies*) | ◊ | ◊ | S[mith] (1884) |
| | Strigiformes | Morepork (*Ninox novaeseelandiae*) | ● | ● | Chambers et al. (1955) and Parrish and Gill (2003) |
| Introduced birds | Galliformes | Domestic fowl (*Gallus gallus)* | ● | | Bell (1996) |
| | Halcyonidae | Laughing kookaburra (*Dacelo novaeguineae*) | ◊ | ◊ | O'Brien (1981) |
| | Passeriformes | Blackbird (*Turdus merula*) | ● | | Bell (1996) |
| | Passeriformes | Common starling (*Sturnus vulgaris*) | ● | | Thompson (2000) |
| | Passeriformes | Common myna (*Acridotheres tristis*) | | ● | Whitaker (1972) |
| | Passeriformes | Australasian magpie (*Gymnorhina tibicen*) | ● | ● | Whitaker (1972) and McIlroy (1968) |
| | Strigiformes | Little owl (*Athene noctua*) | | ● | Marples (1942) |
| Native herpetofauna | Rhynchocephalia | Tuatara (*Sphenodon punctatus*) | ● | ● | Walls (1982) |
| | Squamata | Cryptic skink (*Oligosoma inconspicuum*) | ○ | | Patterson (1992) |
| | Squamata | Duvaucel's gecko (*Hoplodactylus duvaucelii)* | | ● | Barwick (1982) |
| | Squamata | McCann's skink (*Oligosoma maccanni*) | ○ | | Patterson (1992) |

(continued)

**Table 6.2** (continued)

| Description | Order | Species | Skinks | Geckos | Source (examples only) |
|---|---|---|---|---|---|
| | Squamata | Otago skink (*Oligosoma otagense*) | ● | | Tocher (2003) |
| | Squamata | Spotted skink (*Oligosoma lineoocellatum* 'Central Canterbury') | ● | | Allison and Desser (1981) |
| | Squamata | Robust skink (*Oligosoma alani)* | | ● | Southey (1985b) |
| Introduced herpetofauna | Anura | Southern bell frog (*Litoria raniformis*) | ○ | | Romijn (2007) |
| Introduced mammals | Artiodactyla | Pigs (*Sus scrofa)* | □ | □ | King (1995) |
| | Carnivora | Domestic cat (*Felis catus*) | ● | ● | Gibb et al. (1969) and Karl and Best (1982) |
| | Carnivora | Domestic dog (*Canis lupis*) | ● | | Whitaker (1972) |
| | Carnivora | Ferret (*Mustela furo*) | ● | ● | Fitzgerald (1964) and Whitaker (1972) |
| | Carnivora | Stoat (*Mustela erminea*) | ● | ● | King and Moody (1982) |
| | Carnivora | Weasel (*Mustela nivalis vulgaris*) | ● | ● | King and Moody (1982) |
| | Eulipotyphla | European hedge-hog (*Erinaceus europaeus*) | ● | ● | Jones et al. (2005) |
| | Rodentia | House mouse (*Mus musculus*) | ● | | Pickard (1984) |
| | Rodentia | Kiore (*Rattus exulans)* | ● | ○ | Bettesworth (1972b) and Dick (1985) |
| | Rodentia | Norway rat (*Rattus norvegicus*) | ● | ○ | Bettesworth (1972a) and Dick (1985) |
| | Rodentia | Black rat (*Rattus rattus)* | ○ | ○ | Towns et al. (2006) |
| Native invertebrates | Scolopendromorpha | Giant centipede (*Cormocephalus rubriceps*) | ● | ● | Southey (1985a) |

(continued)

**Table 6.2** (continued)

| Description | Order | Species | Skinks | Geckos | Source (examples only) |
|---|---|---|---|---|---|
| | Coleoptera | Carabid beetle (*Megadronas hanmerensis*) | ● | | Whitaker (1972) |
| | Araneae | Katipo spider (*Latrodectus katipo)* | ● | | Lettink and Patrick (2006) |
| Introduced invertebrates | Hymenoptera | Common wasp (*Vespula vulgaris*) | □ | □ | Thomas (1987) |
| | Hymenoptera | European wasp (*Vespula germanica*) | □ | □ | Thomas (1987) |

*Filled circle* = recorded actively preying upon lizard and/or in stomach contents, scats and/or by stable isotopes; *unfilled circle* = inferred as in diet by authors and/or where lizard numbers decrease in the presence of organism; *diamond* = where authors record 'lizards' in diet and therefore may be a gecko, skink or both; *square* = where stated as predators, but evidence has not been provided; *asterisk* = extinct

## 6.6 Conclusions

With around half (45 %) of the 104 endemic species of lizard in New Zealand yet to be formally described, assumptions of biology and ecology have often been made about species based on the ecology of similar, well-known species (e.g. activity period of geckos). What we do know for most species are broad generalisations, with some overlap among a few species, and a few in-depth studies. We can safely conclude that nearly every available habitat from coast to mountain top, and from north to south, has at least one lizard species present. High levels of sympatry exist in some locations, particularly offshore islands where these species partition resources at spatial, temporal and trophic scales. However, some species also show competition and/or aggression and may even prey upon each other. New Zealand lizards appear to have a highly opportunistic dietary strategy, eating whatever is available in the environment, although a few appear to specialise at certain times of the year (e.g. *O. grande* eating flower petals). The lizards of New Zealand also appear to form a key component of the diet of many native and introduced species. Many lizards will form aggregations, and these may be family groupings; parental care is also possible.

For all these trends and generalisations, we still need more information to enable trends in ecology, behaviour and evolution to be described. Additionally, increased understanding of such a large and diverse group of New Zealand's fauna may shed light on the evolution of New Zealand's largest vertebrate group (Towns et al. 2016) and provide much needed information for their effective conservation in situ. Although a daunting prospect, we challenge researchers to continue

collecting, recording and (importantly) publishing various aspects of the ecology of all species. Some particular areas of research that would benefit from more data have been scattered throughout the text, as a starting point for future studies.

**Acknowledgements** We are grateful to Ben Bell, Anna Carter, Sarah Herbert, Zoë Lennon, Sue Keall, Riki Mules, Nicky Nelson, Stephanie Price, Patty Ramirez and Chris Woolley, for comments on the draft chapter. We also thank KC (Kevin) Burns, Alison Cree, Rod Hitchmough and Marieke Lettink for useful discussions and thank Alison Cree and Riki Mules for their personal communications. Finally, we are very grateful to the following for permission to use their photographs: Marieke Lettink, Riki Mules, Rod Morris, James Reardon and the New Zealand Department of Conservation Grand and Otago Skink Recovery Programme.

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