

# Chapter 11

## General Ecology of Patagonian Lizards



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**Abstract** Reptiles have physiological, morphological, and behavioral adaptations that allow them to survive in desert environments, at high altitudes and in cold climates, such as the Patagonia region in southern Argentina. Knowledge of the ecology of Patagonian lizards is limited and fragmentary. The objective of this chapter is to present a synthesis of the current state of knowledge of the ecology of Patagonian lizards with regard to the use of (1) spatial resources (home range, use of microhabitats), (2) temporal resources (daily and seasonal patterns of activity), and (3) trophic resources (diet and nutrition strategies). We also discuss inter- and intra-species interactions, including predation, seed dispersal, parasitism, behavior, and resource partitioning.

**Keywords** Diet · Habitat · Use time · Behavior · Predation · Parasitism · Seed dispersal · Competition · Resource partitioning · Teiidae · Liolaemidae · Phyllodactylidae · Leiosauridae

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## 11.1 Introduction

The structure of communities is modeled on both historical and ecological factors. Ecological factors mainly include interactions among sympatric species and their relationships with the local environment, which in some cases can result from the segregation of the basic resources utilized by the species (food, microhabitat, and activity time; Pianka 1973; Schoener 1974; Mesquita et al. 2015; Winck et al. 2016). In addition, differences between how sympatric species utilize available resources may be influenced by the community itself (ecological factors) and/or can be a reflection of an historic divergence (historical factors; Vitt et al. 1999; Vitt and Pianka 2005; Pinho Werneck et al. 2009). Availability and resources acquisition may vary in time and space, in accordance with behavior of consumers, temporal differences in activity, and use of microhabitats (Winemiller and Pianka 1990). The dimensions that make up the ecological niches of lizards have evolved in tune with changes in their life histories and the patterns have been repeated. For example, lizards from the Australian desert resolve problems in the same way that African and American lizards do, even when they are not phylogenetically related (Pianka et al. 2017).

Although there is consensus about the need and importance of understanding these aspects of the herpetological communities in Argentina and Chile, and particularly in Patagonia, this information is scarce. There are only a few studies on some species with data that is frequently sparse. The objective of this chapter is to compile this information and integrate it in line with the aforementioned central concepts, in other words to present the data currently available on the use of spatial (home range, microhabitats), temporal (daily and seasonal patterns of activity), trophic (diet and nutrition strategies), and inter- and intra-species interactions (predation, parasitism, seed dispersal) and behavior.

## 11.2 Behavior and Activity

### 11.2.1 Behavior

The ecology of behavior is an enormous field of study that includes movements, social interactions, foraging, communication, and escape from predators, among others (Vitt and Caldwell 2013; Cooper and Blumstein 2015). Behavioral decisions that individuals make ultimately influence their aptitude, as they determine if an individual will be able to compete within its species' social system, avoid predators, or successfully find food (Vitt and Caldwell 2013). Within this field, communication is essential for understanding many other aspects, such as territorial defense, mate choice, conflict resolution, foraging, or antipredatory behavior (Font et al. 2010). In general, animals communicate using signals that can be visual, auditory, chemical, or tactile. In lizards, the chemical and visual signals are the most studied;

however, there are some studies that focus on auditory signals (Pough et al. 2001; Labra 2008). Chemical signals (pheromones), dependent on the vomeronasal organ (Labra et al. 2005; Labra 2008; Mason and Parker 2010), play a fundamental role in many aspects of reptile biology, sexual recognition (Cooper 1994; Labra and Niemeyer 1999), territory marking (Halloy and Robles 2002; Fox and Shipman 2003), avoidance of agonistic encounters (Cooper and Vitt 1987; Halloy and Halloy 1997; Labra 2006), aiding in the location of shelter, detection of predators, selection of microhabitat, foraging, communication, and recognition of conspecifics (Labra et al. 2001b; Font et al. 2010; Vitt and Caldwell 2013). Different organs, femoral, precloacal, or urodaeal glands, can produce pheromones (Cooper and Trauth 1992; Cooper 1994; Sánchez-Martínez et al. 2007; Labra 2008). Less specific sources can also be involved such as the exudates of the body surface and feces (Mason and Gutzke 1990; López et al. 1998; Bull et al. 2000; Aragón et al. 2006; Labra 2008).

A Patagonian lizard as *Liolaemus lemniscatus*, for example, like in other *Liolaemus* species, displays a strong response to odors coming from individuals of the same species, that is, its exploratory behavior increases through tongue and head movements (Labra 2011). This could indicate that odors from conspecifics are relevant social signals and that chemical stimulants are involved in the recognition of species, a fact that could aid in maintaining the integrity of species and their reproductive isolation (Labra et al. 2001a; Johansson and Jones 2007; Smadja and Butlin 2009; Labra 2011). Chemical signals and their recognition could play an important role in the diversification of *Liolaemus*, as well as in maintaining its high diversity (Labra 2008). In the different environments of Patagonia, lizard assemblages occur with numerous species of *Liolaemus* living in syntopic conditions and with similar ecological and morphological characteristics, so the recognition of specific chemical signals would have a predominant role in reproductive isolation (Labra 2008). This has been documented in *Liolaemus bellii*, *L. jamesi*, and *L. lemniscatus*, species that differentiate between secretions of sympatric and allopathic conspecifics, suggesting that in sympatric conditions the possibility for hybridization between these *Liolaemus* species is low (Labra et al. 2001b; Labra 2008).

On the other hand, pheromone bioassays for *Liolaemus tenuis* (Fig. 11.1a) demonstrate that their fecal matter contains pheromones utilized for self-recognition, a fact that can be seen in individuals that present a lower number of tongue-flicks on rocks containing their own fecal matter, as opposed to rocks containing the fecal matter of other lizards or the control group. Likewise, *L. tenuis* males do not discriminate between their own precloacal secretions and those of other males, so the authors propose that secretions convey information to males of a “male presence” (Labra et al. 2002). Possibly, males make a latter finer recognition through feces. Alternatively, precloacal secretions may have evolved to convey information mainly detectable or relevant for females or that they convey important information mainly during the breeding season.

Some behaviors may be modeled by each sex within a species, as has been observed in *Liolaemus nitidus* (Fig. 11.1b). This is the case of responses observed in the presence of odors from a conspecific, which trigger greater chemical exploration in males as evidenced by shorter latency with the first hit of the tongue



**Fig. 11.1** (a) *Liolaemus tenuis*, male (front) and female (back). (b) *L. nitidus* with broken tail (Chile). (c) *L. cuyumhue* sand-diving. Black arrows mark dorsum and tail. (d) *L. chiliensis*. (e) *L. curicensis* (Chile)



(Troncoso-Palacios and Labra 2012). This difference in reaction may be influenced by territoriality, as males experience greater selective pressure to recognize and react with individuals of the same sex (Troncoso-Palacios and Labra 2012). In contrast, in the presence of unknown odors or those of predators like snakes, *L. nitidus* responds by shaking its tail for a prolonged period of time or with “slow-motion” actions; both of these strategies help to ward off an attack on its tail by predators, either by losing the tail through autotomy or by reducing its detectability, respectively (Bateman and Fleming 2009; Troncoso-Palacios and Labra 2012). On the other hand, it has been observed that *Liolaemus* does have the ability to detect chemical secretions of snakes, but its responses are dependent on the predation pressure experienced by the species in their natural habitat (Labra 2008). *Liolaemus lemniscatus*, sympatric with the snake *Philodryas chamissonis*, reduces chemical exploration when exposed to snake secretions and shows a high frequency of anti-predatory behaviors, which would reduce its detectability by a predator; on the contrary, *L. fitzgeraldi*, allopatric to *P. chamissonis*, does not show any sign of recognition of and behavior to secretions of the snake (Labra and Niemeyer 2004).

Regarding visual communication, two types of signals have been described in lizards: patterns of coloration and stereotyped movements. The first is generally linked to nuptial coloration or sexual selection, as in many *Liolaemus*, which reflects their reproductive state (e.g., *L. tenuis*; Vidal et al. 2007; Fig. 11.1a), or they may reflect dominance between males, as in *Liolaemus sarmientoi* where males with red coloration are more aggressive during agonistic encounters than those with yellow coloration (Font et al. 2010; Fernández et al. 2018). However, in another species *Liolaemus xanthoviridis*, individuals of both sexes are polymorphic in dorsal coloration (Escudero 2016) and ventral melanism (Escudero et al. 2016), but no evidence was found that this polymorphism represents different reproductive strategies linked to visual signals. Many lizards have vision in the near UV (e.g., Macedonia et al. 2000; Fleishman and Persons 2001; Font and Molina-Borja 2004; Molina-Borja et al. 2006; Whiting et al. 2006), that is, they are capable of perceiving ultraviolet radiation which improves the visibility of their coloration patterns, patterns which are only visible for receivers who have a visual system sensitive to that part of the spectrum (e.g., Harosi 1985; Burkhardt 1989; Yokoyama and Shi 2000; Hunt et al. 2001). The ability to see in the UV is a potentially important route for both intraspecific and interspecific communication and subject to sexual selection. The presence of a photopigment sensitive to UV has been confirmed in 13 species of iguanids, five geckonids, and four chameleons (Fleishman et al. 1993, 1997; Loew 1994; Ellingson et al. 1995; Loew et al. 1996; Bowmaker et al. 2005). In males of three species of *Liolaemus* lizards, *L. grosseorum*, *L. darwinii*, and *L. ruibali*, it has been detected the presence of coloration in the UV range in blue scales located in different parts of the body (Salica and Halloy 2010). However, there is no data regarding the ability of these lizards to perceive this type of coloration. In birds and reptiles, it has been recorded that some species are dichromatic in the visible and ultraviolet spectrum (e.g., Mays et al. 2004), while in others the dichromatism is only found in the ultraviolet region (e.g., Hunt et al. 1998; Thorpe and Richard 2001; Molina-Borja et al. 2006; Pérez de Lanuza and Font 2007). In *L. xanthoviridis*, males and

females with similar coloration (e.g., “yellow”) could be dimorphic in the UV spectrum (Escudero 2016). Several studies have shown that UV colorations are important in intrasexual competition and in the choice of partners in birds, fish, and invertebrates (e.g., Siitari et al. 2002; Losey 2003), but their possible communicative function in reptiles remains relatively unexplored.

On the other hand, there are stereotyped movements. These are very important components of animal communication since deployments usually have a unique “signature” that allows conspecifics to identify each other, allowing individuals to focus on new rivals and not waste energy on known enemies (Husak and Fox 2003). The most common are the headbob display, the forelimb wave, and the tail movements (Font et al. 2010; Halloy et al. 2013). These movements, taken together or separately, are specific to each species and provide information about territoriality, mating, and antipredatory alerts, among other aspects (Carpenter 1978; Martins et al. 2004). They also provide information about the identity of the species, sex, reproductive state, and even individual identity (Halloy et al. 2013). Headbobs are easily distinguished as a series of stereotyped movements of the head up and down, sometimes accompanied by the trunk or by specific body positions such as an extension of the chin or raising of the tail (Martins et al. 2004). Headbobs have been observed in various Patagonian lizards, including *Phymaturus calcogaster* and *P. zapalensis* (Halloy et al. 2013), and in several *Liolaemus* species, including *L. elongatus*, *L. pictus*, *L. cuyanus*, *L. lobo*, *L. lemmiscatus*, *L. darwini*, *L. kingii*, *L. lineomaculatus*, *L. petrophilus*, and *L. xanthoviridis*, among others (Martins et al. 2004; Labra et al. 2007a; Halloy et al. 2013; Escudero 2016). For these lizards, a relatively simple headbob has been described, which may be accompanied by additional visual displays such as forelimb wave, tail movements, and tongue licking, in order to enrich possible messages to conspecifics (Martins et al. 2004; Labra et al. 2007a; Labra 2011; Halloy et al. 2013). Forelimb waving consists of a circular movement of one frontal extremity (though sometimes both frontal extremities are involved) and is generally associated with interactions between males of the same species or with mating behavior (Halloy and Castillo 2006). Some authors have suggested that these movements could indicate subordination when carried out slowly (“submissive wave”) and dominance when carried out quickly (“challenging wave”; Carpenter et al. 1970; Brattstrom 1971). Likewise, Vicente (2019) posits that forelimb waving could function as a social signal, as a submissive signal, or as a pursuit-deterrent signal in *Liolaemus pacha* (a species included in the *Liolaemus darwini* group). Halloy and Castillo (2006) described forelimb waving in 11 *Liolaemus* species and they distinguished two types of movements: a simple movement which involves a single frontal extremity and a more complex movement which involves both frontal extremities. To complete this second complex movement, individuals lower their bodies to the ground and then lift both extremities with a circular waving movement. The latter was observed in *Liolaemus monticola* and *L. pictus*; the former, with more intense movements, was less frequent but was observed in the majority of the species, including *L. monticola*, *L. pictus*, *L. elongatus*, *L. cuyanus* (Halloy and Castillo 2006), and *Liolaemus lobo* (Martins et al. 2004). The tail movement consists of vibrations and horizontal movements of the tail (López and

Martín 2001, 2002; Trigosso-Venario et al. 2002; Aragón et al. 2006) and is usually associated with a behavior of submission or stress. This deployment may be accompanied by a dorsal flattening display, which implies a dorsal-ventral flattening of the body in such a way that the entire ventral surface is in contact with the substrate (Radder et al. 2006).

Another stereotyped behavior, specific to each species and common in some Patagonian lizards, is submersion in sand, inferred to be an escape behavior or preparation for periods of inactivity (Halloy 1995). This behavior has been described for *Liolaemus boulengeri*, *L. canqueli*, *L. cayanus*, *L. darwini*, *L. donosobarrosi*, *L. fitzingerii*, *L. grosseorum*, *L. melanops*, and *L. xanthoviridis* and for the sand dune lizards *Liolaemus wiegmanni* and *L. multimaculatus* (Halloy 2005; Kacoliris et al. 2009b), but it is present in all members of the *L. wiegmanni* group (e.g., *Liolaemus cuyumhue*; Fig. 11.1c). Though this behavior does have its particularities for each species (e.g., submersion time, tail movement, surface scratching, or smelling), in general these species first submerge their heads in the sand, pushing themselves with their hind limbs and placing their forelimbs along the length of their bodies, becoming invisible once their entire bodies are covered (Halloy 2005). Furthermore, behavioral characteristics, such as submersion in sand, provide information that can be used to reconstruct a phylogeny in and of themselves or together with other morphological, genetic, or ecological characteristics (Halloy et al. 2013). Based on 12 polymorphic characteristics of submersion behavior in 19 *Liolaemus* species belonging to the same monophyletic group (*L. boulengeri*; sensu Etheridge 1995), Halloy et al. (1998) defined three modes of submersion in sand: lizards that dig (slow), lizards that slither (medium), and lizards that dive into the sand (fast). This last behavior is the most efficient, and it is a characteristic behavior of lizards specialized in dune environments, like *Liolaemus multimaculatus* (Kacoliris et al. 2009a). The similarities within a group could indicate instances of adaptive convergence, while the differences in the modes of sand submersion (head/tail movements and time) in similar situations could reflect the effects of self-restrictions over the course of a species' life history (Halloy et al. 1998).

Lastly, two little-known but interesting behavioral displays are worth mentioning. One is the ocular protrusion observed in various species in captivity, among them *Liolaemus chiliensis* and *L. gravenhorstii*, which could be involved in ocular cleaning, a hypothesis only partially accepted (Reyes-Olivares et al. 2016), or as a thermoregulatory mechanism as it is commonly observed in lizards put through preferred temperature or critical maximum temperature experiments, as is the case with *L. parvus* and *L. ruibali* (first author personal observation). However, Reyes-Olivares et al. (2016) rule out the thermoregulatory hypothesis and propose that the eye-bulging might be modulated by other factors, mainly in conditions of captivity. The other is a distinctive cleaning behavior which has been recorded for a *L. tenuis* male that rubbed part of his head against the spines of the plant *Echinopsis chiloensis*. It would be interesting to study if this is a stereotyped behavior of the species and if it may be a way of cleaning residue or ectoparasites or a territorial behavior (Ramírez Alvarez 2015).

Within the communication behaviors, vocalization is fairly widespread in other groups of vertebrates, such as amphibians, birds, and mammals, but is less frequent in reptiles. However, studies and reports on acoustic communication in lizards do exist, mainly for Gekkonidae (Russell et al. 2000; Tang et al. 2001; Regalado 2003; Young et al. 2014; among others), some species of Leiosauridae (Frost et al. 2001; Labra et al. 2007b; Laspiur et al. 2007; Reyes-Olivares and Labra 2017), and isolated recordings of Liolaemidae (Carothers et al. 2001; Pincheira-Donoso 2002; Labra et al. 2013). In this sense, lizards respond to predators in diverse ways, among which vocalizations can be interpreted as signals of intimidation, warning, or stress, as well as calls for aid (Greene 1988; Carothers et al. 2001; Labra et al. 2016). In *Diplolaemus bibronii* and *D. sexcinctus*, distributed in the Patagonian steppe of Argentina and Chile, a sharp sound has been described as a violent expulsion of air when disturbed, accompanied by aggressive postures and tail movements, which would correspond to a distress call (Reyes-Olivares and Labra 2017). In *Phymaturus vociferator*, for example, two types of vocalizations were shown to be emitted. The first is a moderate sound, probably of guttural origin, for which lizards do not open their mouths. They make this sound when they are being manipulated or removed from their hiding places in crevices, that is, situations of prolonged stress. The second type of vocalization is similar to that recorded for *Leiosaurus* and *Pristidactylus* and is characterized by violent expulsions of air from a mouth which is completely open, producing a high-pitched whistle-like sound (Pincheira-Donoso 2002, 2004). This whistle is accompanied by an upright defensive posture with an open mouth and is produced in situations of sudden stress (Pincheira-Donoso 2002). On the other hand, in the genus *Liolaemus*, vocalization behaviors have been reported for *Liolaemus curis* (Núñez and Labra 1985) and the crying lizard *Liolaemus chiliensis* (Fig. 11.1d), probably produced by the larynx as an antipredatory response (Carothers et al. 2001). These lizards emit a sound when captured by a predator, which could warn conspecifics of the threat or create opportunities for escape (Labra et al. 2013). Conspecifics can reduce their risk of being captured by reacting to the cry with immobility or escape behaviors (Hoare and Labra 2013). Prolonged immobility reduces *L. chiliensis*'s possibility of being detected by its most frequent predators, the raptor *Falco sparverius* and the snake *Philodryas chamissonis*, as both employ a "sit and wait" hunting strategy, meaning that *L. chiliensis* reduces its risk by becoming immobile upon hearing the cry (Labra et al. 2016).

As will be mentioned in upcoming sections of this chapter, in the Patagonia region, lizard species are exposed to numerous predators, including arachnids, birds, snakes, and even other lizards. To cope with this situation, these lizards must utilize a variety of antipredatory strategies to reduce their risks of being captured, among which are tail autotomy; chemical, visual, and auditory communication; immobility; and/or escape. The initial escape distance (or critical distance), the escape latency, and the escape distance (distance from initial position to the closest shelter) have been used as indicators of lizards' predatory risk (Martín 2002; Kacolicis et al. 2009a; Cooper and Blumstein 2015; Fava and Acosta 2018). These critical and escape distances can be linked to individuals' weight, body temperature, and the perch height that saxicolous species select (Núñez 1996). For example,



*Liolaemus curis* selects rocks at high altitude and as such has greater possibilities of seeing predators far away. Consequently, its initial escape distance is greater than that of the sympatric lizard *L. curicensis* that uses rocks at lower heights. Likewise, *L. curis* looks for shelter in the nearest microsites (least escape distance), while *L. curicensis* (Fig. 11.1e) prefers to use rocks as shelter or bushes if it is on the ground (Núñez 1996).

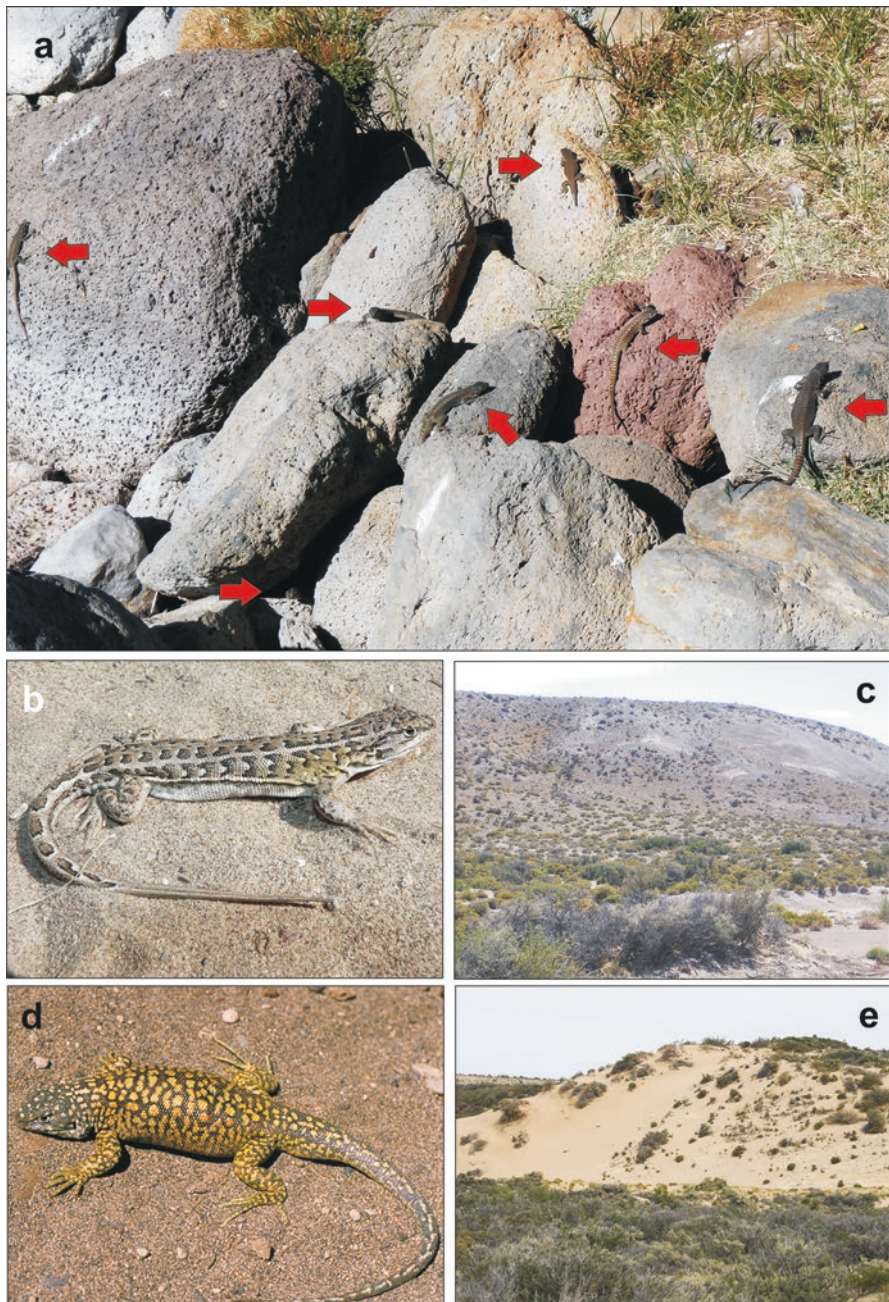
Escape behaviors can be affected by modifications in habitat structure, meaning vegetation coverage, as consequence of grazing, deforestation, and the introduction of new species of vegetation, among other causes (Amo et al. 2007; Anderson and Burgin 2008; Pietrek et al. 2009; Stellatelli et al. 2015). Two saxicolous species *Liolaemus elongatus* and *Phymaturus patagonicus*, inhabit the Patagonian steppe, both specialists in this habitat, along with *L. bibronii*, a versatile lizard in terms of ecological requirements and a generalist in the use of habitats (Scolaro 2005). Pietrek et al. (2009) compared these lizards in terms of their proportions of stops on uncovered ground in escape situations in experimental areas with different percentages of coverage. These authors observed that both *L. bibronii* and the specialist species made more stops on uncovered ground in situations with less vegetation coverage. In addition, all three species were captured more easily in this situation, though with *L. elongatus* and *P. patagonicus* being more susceptible than *L. bibronii*. Therefore, one of the costs associated with spread is an increase in predation risk, and in this sense low levels of vegetation coverage mean greater susceptibility to predation as exposure of the lizard is increased (Pietrek et al. 2009). On the other hand, an increase in vegetation coverage through forestation with non-native plants could also lead to changes in escape behaviors and could increase predatory possibilities (Stellatelli et al. 2015). In a study carried out in coastal dunes with both modified (non-native forestation) and natural (no forestation) habitats, Stellatelli et al. (2015) observed an increase in predatory pressure for lizards at the modified sites. Consequently, *Liolaemus wiegmanni* and *L. multimaculatus* make certain adjustments in their antipredatory behavior (Stellatelli et al. 2013, 2015). *Liolaemus wiegmanni*'s initial escape distance is greater at modified sites than at the non-forested sites, while *L. multimaculatus*'s initial escape distance is shorter at the modified sites, probably due to the fact that it employs a sand submersion strategy to reduce predation risks (Stellatelli et al. 2015).

The social behavior in lizards covers a great variety of behaviors, among which stand out parental care, reproductive courtship, cooperative care of offspring, custody behavior, aggressiveness, territoriality, and aggregation (Fox et al. 2003). The parental care can increase their offspring's physical aptitude by providing protection and/or nutrition, which in turn favors the survival of their descendants (Shine 1988; Somma 1990; Pike et al. 2016). The Patagonian region (north and south) implies rigorous environmental conditions for lizards, as well as great predatory pressure (see Sect. 11.3.2) and competition for resources. For this reason, parental care is an optimal strategy for guaranteeing the survival of one's offspring, a strategy that has been observed in some, generally viviparous, species of the family Liolaemidae (Halloy et al. 2013; Cabezas-Cartes et al. 2018a). In *Liolaemus elongatus*, females and their offspring occupy the same shelter for various days after

birth, which provides to the newborn lizards thermal and hydrological stability during the cold, dry Patagonian nights (Halloy et al. 2007). It has also been observed that upon leaving the shelter, females of this species cover their newborn offspring, different from what has been recorded for *Phymaturus calcogaster* when females put their offspring on their backs; both behaviors probably serve to distract predators (Halloy et al. 2013). Two types of behaviors have been described when *Phymaturus spectabilis* females find themselves and their offspring under threat in experimental conditions (Cabezas-Cartes et al. 2018a). In the presence of a terrestrial predator such as *Pristidactylus nigroiugulus*, they display active behaviors such as headbobs, tail elevation, and escape, whereas when the threat is aerial, females reduce their activity and spend more time in crypsis near their offspring (Cabezas-Cartes et al. 2018a). Nevertheless, in field conditions in the Puna region, *Phymaturus williamsi* (non-Patagonian species) flees to nearby shelters when it detects the presence of a bird of prey and varies its time of reappearance depending on the size of the predator (Fava 2018; Fava and Acosta 2018). However, the similar behaviors observed in *Phymaturus* (Halloy et al. 2013) allow us to hypothesize a common pattern of parental care related to *Phymaturus*'s high reproductive investment (Cabezas-Cartes et al. 2018a).

One social behavior relatively unexplored in Patagonian lizards is aggregation. Alzamora et al. (2010) reported aggregation findings for *Phymaturus vociferator* in Laguna del Maule, Chile, in which they found 37 individuals, including males, females, juveniles, and newborns, under a single rock. This behavior could allow these lizards to survive the rigorous winter conditions of high-altitude environments (Alzamora et al. 2010) and is probably common for other *Phymaturus* species. A similar behavior has been frequently observed in several species of the *Phymaturus patagonicus* group as well as in species of the *Liolaemus elongatus* complex (Avila et al. unpublished, Fig. 11.2a). Clearly, the aggregation affects the thermoregulatory behavior of a lizard; however, the effect would not always represent an advantage for the individual. For example, in *Pristidactylus torquatus* and *Pristidactylus volcanensis*, the presence of conspecifics affects the thermoregulation of individuals, lizards which are solitary and territorial, and as such, social influence could be a factor involved in changes in body temperature (Labra 1995). Taking into account Patagonia's extreme environmental conditions, with low temperatures and snowfall in winter and great thermal amplitude during the lizards' active seasons, it would be interesting to evaluate aggregation behaviors in other Patagonian species as a strategy for coping with these extreme conditions.

The recognition of familiar individuals, primarily in territorial species, is a social behavior that could help to reduce the frequency and intensity of aggressive encounters, stabilizing social systems and reducing the costs of preserving territory (Fox and Baird 1992; Hanley et al. 1999; Vitt and Caldwell 2013). For example, *Liolaemus tenuis* males are territorial and tend to tone down their aggressive behavior in the presence of a familiar individual as opposed to an unknown conspecific (Trigoso-Venario et al. 2002), responding to the "dear enemy" phenomenon (Ydenberg et al. 1988). Likewise, recognition of a familiar individual is lost after a prolonged period of time without social interaction, which is relevant for interactions with "floating"



**Fig. 11.2** (a) Aggregation of *Liolaemus elongatus* at the Area Natural Protegida Tromen, Neuquén, Argentina. Red arrow marks adult individuals (courtesy of Daniel Paz Barreto). (b) *L. inacayali*, male. (c) Habitat of *L. inacayali* near the type locality, in Río Negro Province, Argentina. (d) *Liolaemus xanthoviridis*. (e) Habitat of *L. xanthoviridis* at Isla Escondida Bay, Chubut, Argentina



males or neighbors who lose their territory and later attempt to fight to recover it (Trigoso-Venario et al. 2002).

### 11.2.2 Use of Time and Space

A fundamental aspect in lizard ecology is related to the different ways in which species make use of spatial and temporal resources (Reilly et al. 2007). Knowledge of the rhythm of temporal, daily, and seasonal activity, together with the use of space, can provide details about the behavior, thermal requirements, and thermoregulatory mechanisms of a species (Chap. 13); a large part of the activity of any organism depends on the thermal characteristics of its environment (Labra et al. 2001c; Smith and Ballinger 2001; Villavicencio et al. 2002; Kacoliris et al. 2011). Likewise, knowledge of the use of space is important because in this way we understand the resources potentially available to lizards, such as food, water, mates, thermal availability, nesting sites, and shelters, among others (Begon et al. 1990; Pough et al. 2001). That is, lizard species perform movements and select sites that optimize their subsistence, survival, and reproduction (Pough et al. 2001; Kacoliris et al. 2011; Vitt and Caldwell 2013).

Patterns of daily and seasonal activity of species that inhabit the Patagonian plateau are limited to months with suitable temperatures. Most of the Patagonian lizards are limited to the spring and summer months, from September to March, while between April and August, they are in a period of hibernation. But in Peninsula Valdés, *Liolaemus gracilis* and other *Liolaemus* (probably *L. darwini* and *L. melanops*) have been observed in July or August. Winter activity in Patagonian lizards could be more common than expected but is an issue not studied until now. Among the species for which characteristics of population structure are known, we find *Liolaemus inacayali* (Fig. 11.2b) present in an ecotone zone between Patagonian steppe and the Monte, in Río Negro Province. This region is characterized for its dry, desert climate; an average annual temperature of 4 °C; absolute minimum and maximum temperatures of 1 °C and 10 °C, respectively; annual precipitations of less than 200 mm (mostly snowfall); and winds out of the west at 100 km/h. This species remains active from mid-September, the end of the southern winter, until March, the beginning of autumn. The first age group to emerge from its winter lethargy are the juveniles, born the previous season. Later, adult males and females appear. Births take place in February, adult activity declines, and youths remain active, with this last group being the last to retire at the beginning of autumn (Acosta et al. 1996). The microenvironment mainly utilized by *L. inacayali* adults is the sand base of bushes, used as a site for feeding, protection, and the digging of caves for shelter, in addition to small rocks (Fig. 11.2c). This species is rarely found in rocky areas; nevertheless, young individuals can be found in areas with little or no vegetation coverage. Their daily activity is unimodal and they are heliothermal. This species shares its habitat with two other species, *Liolaemus bibronii*, with a lower population density living along the edges of the plateau, and *Leiosaurus belli*,

also found in the sand base of bush plants, though without temporal overlap (Acosta et al. 1996).

*Liolaemus xanthoviridis* is another Patagonian species distributed around the Plateau of Montemayor, in Chubut Province, Argentina. The period of activity of these arenicolous lizards begins in late September to early October and continues until mid- to late March (depending on environmental temperature). Between October and December, matings and oviposition of eggs occur, while between January and March, the emergence of the first juveniles marks the moment that the hatching occurs. For *Liolaemus xanthoviridis*, the vegetation cover would be of great importance at the time of using a particular microhabitat, since the microhabitat that it occupies presents on average 68% of total vegetation cover (Escudero 2016) (Fig. 11.2d).

Another species that inhabits the Patagonian plateau is *Homonota darwini* (Fig. 11.3a), the most southerly nocturnal lizard in the world. Due to the harsh climatic conditions prevailing in the region, adequate shelter is limited. The performance and survival of nocturnal lizards depends on the thermal quality of their diurnal shelter. A study of this gecko's use of shelter shows that shelters with higher temperatures were always selected, independent of the rocks' size or thickness. These results demonstrate the importance of a shelter's thermal quality for reptiles living in extreme environments (Aguilar and Cruz 2010). It is very difficult to find *H. darwini* in natural environments, but instead it is very easy to find them in garbage (Fig. 11.3b), building debris, or even shorebirds remains (Fig. 11.3c), or trapped with other lizards species, in artificial ponds made by oil extraction companies (Fig. 11.3d).

It seems that the only *Liolaemus* species with occasional nocturnal activity in cold regions of the Patagonian Andes is *L. tenuis* (Avila and Morando 2015) (Fig. 11.3e), a lizard widely distributed in central Chile, though in Argentina it only inhabits a small area of Andean-Patagonian forest in the province of Neuquén. Other species of *Liolaemus* are only active for a brief period at dusk in the Monte region. However, the vast majority of *Liolaemus* lizards have daytime activity, with bimodal patterns (activity in the morning and afternoon, e.g., *L. lemniscatus*, *L. monticola*, *L. tenuis*) or unimodal patterns (activity from midmorning to early afternoon), as is the case for *L. schroederi* and most of the species of the Teiidae family that peak at the hot middle of day (Pianka 1969; Fuentes 1976; Belver and Avila 2001).

The wide diversity and versatility of species in *Liolaemus* allow us to identify different types of microhabitats selected by lizards, such as rocks (e.g., *L. monticola*, *L. curi*, *L. nitidus*), trunks and trees (e.g., *L. tenuis*, *L. pictus*), open ground (e.g., *L. lemniscatus*, *L. curicensis*), under shrubs (e.g., *L. schroederi*, *L. chiliensis*), and sand dunes (e.g., *L. multimaculatus*, *L. cuyumhue*), among others (Fuentes 1976; Jaksić and Fuentes 1980; Núñez 1996; Avila et al. 2009; Kacoliris et al. 2011). Additionally, Zúñiga et al. (2016) carried out a study in central-southern Chile in which they compared the habitat use of three lizard species, *L. tenuis*, *L. pictus*, and *L. lemniscatus*, in native forests and plantations of *Eucalyptus globulus*, and they evaluated niche segregation at the microhabitat level. They observed





**Fig. 11.3** (a) *Homonota darwinii* with broken and regenerating tail in natural environment. (b) Human garbage used as shelter by *H. darwinii*. (c) *H. darwinii* (red arrow) living in a carcass of a dead shorebird in Playa Colombo, Península de Valdés (courtesy of J. Grummer). (d) Dead lizards trapped in oil rig artificial pond. (e) *Liolaemus tenuis* foraging around a patio light in the night (Avila and Morando 2015). (f) *Lycium* fruits, a common food for some lizard species (courtesy of C.H.F. Pérez). (g) *L. austromendocinus* eating a butterfly in a rocky outcrop near Crucero Catriel, Neuquén, Argentina (courtesy of C.H.F. Pérez). (h) *L. grosseorum* eating a scorpion in the Bajo de Añelo, Neuquén Province, Argentina (courtesy of M.V. Brizio)

higher frequency in the native forest as opposed to the plantations. The three species make a differential use of microhabitats; *L. tenuis* is more associated with trees, *L. lemniscatus* with the ground level, and *L. pictus* with a generalist tendency (Zúñiga et al. 2016).

An individual's preference for a particular microhabitat can affect how it perceives predation risk and therefore its antipredatory behavior (Constanzo-Chávez et al. 2018). The sympatric species *Liolaemus chiliensis* and *Liolaemus nitidus* select different microhabitats and may experience different selective pressures against shared predators (e.g., raptors and snakes). On the one hand, *L. chiliensis* is commonly found basking on bushes, a complex microhabitat that can provide protection against predators, and only reduces its activity in high-risk conditions, while *L. nitidus* prefers open microhabitats at the top of rocks with high exposure to visual predators such as raptors. In this sense, *L. nitidus* reduces its activity and is alerted to a high or low risk of predation (Constanzo-Chávez et al. 2018). Similarly, *Liolaemus curis* (exclusively saxicolous) and *Liolaemus curicensis* (terrestrial-saxicolous), which inhabit a mountain sector with a Mediterranean climate and fluctuating rains where vegetation is squat and xeromorphic, use shelter differently in the presence of predators; *L. curis* flees into crevices, while *L. curicensis* uses bushes for cover. These species are not syntopic but rather allotropic. They live in different spaces and coexist, thanks to their habitats, *L. curis* being restricted to large rocks and *L. curicensis* to small bushes with isolated rocks (Núñez 1996).

In Tierra del Fuego, the world's southernmost region, lives *Liolaemus magellanicus*, in two areas that differ in their appearance, vegetation, and soil, though both are located less than 200 m from the coast. The vegetation at one of the sites is coastal brush with few bushes and plants in thickets. The soil is sandy and dug up by the fossorial rodent *Ctenomys magellanicus* (Ctenomyidae). The other site is a coastal steppe homogeneously covered by *Festuca* sp. grass. Its soil is a sandy-clay mix and fossorial rodents are not present. At the first site, *L. magellanicus* individuals were seen at the entrance of *Ctenomys* dens, and at the second site below debris (Jaksić and Schwenk 1983).

The local spatial distribution of individuals is often described in terms of "home range" (HR) and "territory." The first is defined as the entire area in which an individual performs its daily activities, which includes exploratory movements outside of it and in which it spends most of the time and is not necessarily exclusive or defended (Burt 1943), whereas "territory" is a defended area for exclusive use (Noble 1939; Brown and Orians 1970). Few studies have examined space use in Patagonian species of lizards. In this sense, the Patagonian *Liolaemus melanops* was studied, a medium-sized lizard (90 mm snout to vent length) which is found in low sandy zones and coastal dunes of the provinces of Río Negro and Chubut, Argentina. The study was carried out with a population located in center of Chubut, with no significant differences in average HR for males and females. Moreover, no correlation between body size and the size of the HR was found, though great overlap in the HR utilized by males was observed; this was not the case for females (Frutos and Belver 2007). *Liolaemus petrophilus* presented a similar average home range in males and females with a high degree of inter- and intrasexual overlap. This

important degree of overlap would seem to indicate the lack of territoriality in males and females (Frutos 2009). Opposite results were recorded in a coastal species, and males and females of *L. xanthoviridis* used space differently. Males presented home ranges associated with body size and greater than females. The observed overlapped patterns could indicate that females are territorial, but not males (at least with respect to the complete HR; Escudero 2016). On the other hand, in the Andean cordillera of central Chile, a study on the use of space in populations of seven *Liolaemus* species suggested that the high-elevation lizards (2900 msnm; *L. belli*, *L. leopardinus*) were tolerant of high home range overlap of conspecifics, both males with males and females with females; they found no evidence of territorial social organization. Lizards from low (1200 msnm; *L. monticola*, *L. lemniscatus*) and mid (2300 msnm; *L. schroederi*, *L. nitidus*) elevation sites generally were aggressive; males were intolerant of home range overlap with other males, and females also showed low spatial overlap. These species showed territorial social organization (Fox and Shipman 2003).

## 11.3 Trophic Ecology

### 11.3.1 Diet

Knowledge of trophic ecology, particularly diet, has important implications for our understanding of reptile ecology in general and their functional morphology, ecomorphology, behavior, and physiology. At the same time, in lizards there exist diverse sources of variation in diet due to hereditary features such as body size, biomechanics, activity time, resource availability, sensory abilities, thermoregulation strategies, modes of foraging, and physiological restrictions, among others (Vitt et al. 1997; Vitt et al. 2003; Vitt and Pianka 2007). The description and quantification of diet are principal aspects of studies of a species' ecology (Pianka 1973; Aun et al. 1999; Vitt and Pianka 2007) and are closely related to the availability and abundance of food resources, inter- and intra-species competition, capture abilities, and habitat conditions (Aun et al. 1999; Castro et al. 2013). Studies on what makes up a species' diet have been carried out using a variety of methodologies, which include direct observation of foraging in the field and stomach and feces analysis. Nevertheless, it has been demonstrated that direct observation of stomach and intestinal contents is considerably more precise for the determination of diet than feces observation (Pincheira-Donoso 2008) and field observations, which are often coincidental and random.

In the Argentine and Chile Patagonia, studies of the trophic aspects of lizard species are particularly limited. We only have general data about their trophic niche, taken from notes of particular findings, from some more specific works on diet, and from anecdotal data on natural history in the species' description. Diet composition has only been reported in detail for 21 species (11.04%) of Patagonian lizards, the majority of which are carnivorous (insectivores) and/or omnivorous (Table 11.1).

**Table 11.1** Items recorded in the diet of Patagonian lizards

Species	Arthropods						Chordates				Plant matter			Diet					
	Insecta		Arachnida		Isopoda		Mollusca		Reptile		Bird		Mammal		Fruit	Seed	Flower	Others	
	Diplopoda	Chilopoda	Arachnida	Isopoda	Entognatha	Mollusca	Reptile	Bird	Mammal	Fruit	Seed	Flower	Others						
<i>Liolaemus bibroni</i> <sup>a</sup>	★			★										★	★	★	★	Insectivore/ Omnivore	
<i>Liolaemus burmetsteri</i> <sup>b</sup>	★			★														Insectivore	
<i>Liolaemus crandalli</i> <sup>c</sup>	★														★			Omnivore	
<i>Liolaemus curicensis</i> <sup>d</sup>	★			★											★	★	★	Omnivore	
<i>Liolaemus curi</i> <sup>d</sup>	★			★					★						★	★	★	Omnivore	
<i>Liolaemus cuyanus</i> <sup>e</sup>	★			★											★	★	★	Omnivore	
<i>Liolaemus cyanogaster</i> <sup>f</sup>	★			★														Insectivore	
<i>Liolaemus darwini</i> <sup>g</sup>	★			★														Insectivore	
<i>Liolaemus elongatus</i> <sup>h</sup>	★			★												★		Omnivore	
<i>Liolaemus inaccyali</i> <sup>i</sup>	★														★	★	★	Omnivore	
<i>Liolaemus lemmiscatus</i> <sup>d</sup>	★			★									★					Insectivore	
<i>Liolaemus monticolai</i>	★			★												★	★	Insectivore	
<i>Liolaemus nitidus</i> <sup>k</sup>	★															★		Insectivore	

(continued)

**Table 11.1** (continued)

Species	Arthropods						Chordates				Plant matter			Diet	
	Insecta	Diplopoda	Chilopoda	Arachnida	Isopoda	Entognatha	Mollusca	Reptile	Bird	Mammal	Fruit	Seed	Flower		Others
<i>Liolaemus pictus</i> <sup>1,m</sup>	★			★		★									Insectivore
<i>Liolaemus wiegmanni</i> <sup>n</sup>	★			★											Insectivore
<i>Phymaturus vociferator</i> <sup>p</sup>	★										★				Herbivorous
<i>Phymaturus zapalensis</i> <sup>p</sup>	★													★	Omnivore
<i>Salvator rufescens</i> <sup>q</sup>	★		★		★		★		★		★				Omnivore
<i>Teiuss oculatus</i> <sup>r</sup>	★			★											Insectivore
<i>Homonota darwini</i> <sup>s</sup>	★			★											Insectivore
<i>Homonota horrida</i> <sup>t</sup>	★			★											Insectivore

Data were selected from published sources

References; <sup>a</sup> Belver and Avila (2002); <sup>b</sup> Avila et al. (2012); <sup>c</sup> Avila et al. (2015); <sup>d</sup> Núñez (1996); <sup>e</sup> Moreno Azócar and Acosta (2011); <sup>f</sup> Codoceo (1954); <sup>g</sup> De Viana (1994); <sup>h</sup> Quatrini et al. (2001); <sup>i</sup> Acosta et al. (1996); <sup>j</sup> Ipinza Regla (1985); <sup>k</sup> Jaksic and Fuentes (1980); <sup>l</sup> Ortiz (1974); <sup>m</sup> Vidal (2007); <sup>n</sup> Aun et al. (1999); <sup>o</sup> Celedón-Neghme et al. (2005); <sup>p</sup> Boretto and Ibargiengoytia (2018); <sup>q</sup> López Juri et al. (2015); <sup>r</sup> Acosta et al. (1991); <sup>s</sup> Kun et al. (2010); <sup>t</sup> Aun and Martori (1994)



Some anecdotal data is available from occasional field observations, for example, for *L. austromendocinus* (Fig. 11.3g) or *L. grosseorum* (Fig. 11.3h). In general for *Liolaemus* species, their predominant prey are arthropods, and within this group, the Formicidae family, as several species have been observed eating ants. Ants represent a resource widely available in large densities, reason for which many lizard species choose to exploit them utilizing an active search strategy. The energy cost that this strategy demands is compensated for by the ease of trapping this prey and by its abundance (Quatrini et al. 2001). The diet composition of only one herbivorous species, *Phymaturus vociferator*, is known and includes fruit and vegetation matter, including seeds, and on occasion ant remains (categorized as incidental). This species demonstrates a clear tendency for the consumption of fruits, mainly those of *Calandrinia* sp. (Celedón-Neghme et al. 2005), as opposed to what has been reported for non-Patagonian *Phymaturus*, such as *P. williamsi*, which mainly consumes flowers from the genus *Adesmia*, or *P. punae*, which prefers *Adesmia* stems and leaves (Castro et al. 2013; Córdoba et al. 2015). On the other hand, Boretto and Iburgüengoytía (2018) reported for *Phymaturus zapalensis*, endemic to Laguna Blanca National Park in Neuquén Province, presence of plant matter and insects in the digestive tract of 15 individuals, indicating an omnivorous diet unique in the genus. Boretto and Iburgüengoytía (2018) suggest that a high-energy omnivorous diet could explain an annual reproductive cycle in females of *P. zapalensis*, instead of the characteristic biennial cycle in other species of the genus (Boretto and Iburgüengoytía 2009; Boretto et al. 2018; Castro et al. 2018).

Of the 169 taxa present in the Patagonia region, the great majority (75%) are classified as insectivorous or insectivorous/omnivorous, while strictly herbivorous species are considerably less common, reserved almost exclusively for species of the genus *Phymaturus* and some *Liolaemus* species, such as *L. avilai*, *L. morandae* (Breitman et al. 2011), *L. ceii* (Scrocchi et al. 2010), and *L. silvanae* (Abdala 2012), though serious studies are needed to corroborate this data. A tendency toward herbivorism has been documented for small lizards in cold climates (Espinoza et al. 2004). The availability of animal resources could fluctuate and become limited during certain times of the year in variable and hostile environments such as steppes, the Patagonian coast, and Andean locations which are volcanic and rocky. This implies an additional energy cost in the search for prey. In these cold and variable environments, the use of vegetation resources, which are more stable throughout the year, would be a good foraging strategy. However, herbivorism has additional costs for digestion, as the majority of the energy contained in vegetation matter is in the form of fibrous compounds, such as cellulose. For this reason, herbivores have intestinal specializations that include blinds, intestinal valves, and nematodes in the rear intestine which facilitate the fermentation of fiber components and lengthen digestion retention time, thereby increasing digestive efficiency (Iverson 1982; Stevens and Hume 1998; Castro et al. 2013).

The strategies employed by lizards in their search for food involve ways of obtaining matter and energy needed for growth, maintenance, and reproduction. But this search for food implies both energy and survival costs, because when a lizard is feeding, it may be exposed to predators and because time dedicated to feeding

means time not invested in other activities such as courtship. As such, the foraging strategies that a species employs must be optimal in terms of energy returns (Pianka 1966; Huey and Pianka 1981). Two strategies of food acquisition have been described. In the first, known as the “sit and wait” strategy, the predator waits in a certain location until its prey passes nearby and then “ambushes” the prey. In this case, the energy that an individual requires is little, and an energy gain will depend on the density and mobility of its prey. On the other hand, in the “active foraging” strategy, the predator actively seeks out its prey and as such requires greater energy for the search but is not dependent on the density and mobility of its prey (Pianka 1966). Generally speaking, a generalist and opportunist diet is associated with the “sit and wait” method, while a specialist diet is more closely related to the “active foraging” strategy, as is the case of the majority of species from the Teiidae family, which are frequently observed looking for food between patches of vegetation, digging through fallen leaves and into the ground and sticking their snouts into holes or caves (Acosta et al. 1991). Nonetheless, both of these tactics are the extremes on a continuum of possible strategies for food location, strategies that versatile and opportunistic species like those of the genus *Liolaemus* make use of. Within this group, we observe both generalist (*Liolaemus curicensis*, *L. lemniscatus*, *L. tenuis*, *L. schroederi*) and specialist species (*L. curis*, *L. monticola*) in terms of diet, who employ a “sit and wait” method of foraging (Fuentes 1976; Núñez 1996), to the employment of mixed foraging strategies, as those utilized by *Liolaemus wiegmannii*, *L. bibronii*, *L. inacayali*, or the gecko *Homonota horrida* and *H. darwini*, depending on available resources (Aun and Martori 1994; Acosta et al. 1996; Aun et al. 1999; Belver and Avila 2002; Kun et al. 2010). These changes in feeding behavior can be interpreted to be adaptations to the variability of food resources in the highly unpredictable desert environment, that is, the arid, cold Patagonian steppe, and could favor species with an opportunistic diet in the southern region (Belver and Avila 2002).

Likewise, lizard foraging strategies, diet, and availability of resources also probably vary due to the influence of extrinsic factors such as the seasons and temperature of the environment. As such, it is essential to carry out long-term, annual studies in order to take into account opportunistic changes in species' trophic ecology. Additionally, intraspecific differences (sex and age group) in diet may also exist, as well as among populations of the same species. For this reason, it is necessary to look at these factors in order to have a greater understanding of a species' biology. Studies that evaluate seasonal and intrapopulation changes are limited or nonexistent for Patagonian lizard species. For example, differences in diet composition between age groups and seasons have been observed in *Liolaemus inacayali*. During the spring, juveniles mainly feed on ants and vegetation, while in the summer, their diet is restricted to Diptera and Hymenoptera, and in second place ants. Adults (both males and females) mainly consume vegetation and ants during the first period, while during the second period, Hemiptera become more relevant and vegetation consumption decreases. This age group and seasonal variation is associated with the variation in abundance of food offer on site; for instance, greater consumption of vegetation in the first period could possibly be due to a lower abundance of

arthropods during this time (Acosta et al. 1996). The *Liolaemus pictus* diet is mainly made up of Diptera, Homoptera, Hymenoptera, and Coleoptera, and its composition does not vary among populations at three different sites of the Vicente Pérez Rosales National Park in Chile. This coincides with what Vidal (2007) proposed, although there are variations between locations: *L. pictus* consumes preys in relatively similar quantities in different populations (Vidal and Labra 2008). Nevertheless, the adults of these populations have a higher preference for Coleoptera and arachnids than juveniles (Ortiz 1974). In addition, *L. pictus* has been considered an active forager with an opportunistic diet since it consumes a wide variety of large-size species (19 items; Vidal 2007; Vidal and Labra 2008), similar to the food behavior documented for *L. lemniscatus* (16 items; Núñez et al. 1989).

For two populations of *Liolaemus elongatus*, one at a forest site and the other at a plateau site, Quatrini et al. (2001) did not observe qualitative differences in diet. Both populations are omnivorous, with ants being the fundamental dietary component. They only differ in their second item of importance, Homoptera for the plateau population and seeds for the forest population, as fruits are widely available at that site. Another study on trophic diversity in sympatric species (*Liolaemus lemniscatus*, *L. tenuis*, *L. fuscus*) and different populations of *L. lemniscatus* proposes that interspecific and population variations in diet are determined by variation in the availability of trophic resources, which in turn determines a specialized or generalist diet (Hurtubia 1973). Therefore, geographical variations in biotic and abiotic characteristics can determine populations' variations in predators (Vidal and Labra 2008).

Changes in diet composition between sexes may be due to a decrease in mobility for females during the gestation period (Martori and Aun 1997). As an example, Aun et al. (1999) observed that ants for *Liolaemus wiegmanni* are generally an important component of the diet. However, in the spring, females mainly feed on flies, probably due to the fact that gestation restricts their range of activity to shelter walls, while males, in addition to consuming ants, feed on locusts that they find by roaming about the territory. They also observe that in the winter the secondary prey for females is spiders, which are sedentary, while for males, larvae are important resources for biomass contributions (Aun et al. 1999). Another source of variation in diet, a source that has not been well explored, is the length of the lizard and its head shape. Jaksić and Fuentes (1980) observed that the most abundant prey in the *Liolaemus nitidus* diet are Coleoptera and found that there is a positive association between an individual's length and the length of the consumed prey. They argue that larger individuals have larger snouts that allow them to trap and swallow larger prey. There is also a correlation between the variety of prey consumed and lizard size, as although they do prefer larger prey, they do not stop feeding on smaller prey as well, such as ants. On the other hand, bigger lizards tend to be omnivorous-herbivorous as it is energetically more beneficial for them to feed on small insects (Pough 1973; Moreno Azócar and Acosta 2011), in addition to the fact that the availability of bigger preys is usually limited (Fuentes 1977; Jaksić and Fuentes 1980). Hence, as *L. nitidus* individuals grow, there is a tendency toward herbivorism because as juveniles the availability of small prey in relation to their size is abundant on site, but this is not the case for adults (Jaksić 1978; Jaksić and Fuentes 1980).

As can be seen in the examples presented, diet composition and availability of resources are influenced by various intrinsic and extrinsic factors, a fact which justifies the need for studies that fill in information gaps regarding the trophic ecology of Patagonian lizards. Moreover, the methodological designs of these studies should take into account random factors such as seasonality, environment type, sex, and ontogeny, among others, so as to obtain a greater generalization and understanding of the ecological patterns of species in this region.

### 11.3.2 Predation and Seed Dispersal

From a functional point of view, lizards can be considered fundamental elements of their ecosystems, participating in processes central to the functioning of natural systems, including seed dispersal and pollination, as well as acting as prey for other groups such as raptors, snakes, and other lizards, among others (Acosta et al. 2018). In this sense, seed dispersal is an important part of a plant's life cycle, in which animals may play a determining role as biological interactions between plants and animals could occur and both could benefit. In his review, Godínez-Álvarez (2004) indicates that various species of lizards feed on nectar and fruits and that upon consuming these materials, they could be effectively pollinating flowers or dispersing seeds to sites far from the mother plant. Frugivorous species not only play an important role in seed dispersal; they also have an important impact at the moment of germination, depending on how the seed passes through the lizard's digestive tract (Traveset and Willson 1997; Varela and Bucher 2002). *Teius teyou* is considered a legitimate disperser of viable seeds from the *Ziziphus mistol* plant, as the seeds begin to germinate a few months after passing through the digestive tract. Nevertheless, the greatest benefit this plant receives from having its seeds ingested by *T. teyou* is seed dispersal, demonstrating a "high-quality deposit pattern" (Schupp 1993; Varela and Bucher 2002). Willson et al. (1996) documented frugivorism and seed transport for *Liolaemus pictus*, a species that is mainly described as arboreal. In the analysis of its feces, both *Nertera granadensis* and *Relbunium hypocarpium* seeds are found, and in the case of *Nertera*, the seeds germinated faster after passing through the lizards' digestive tract.

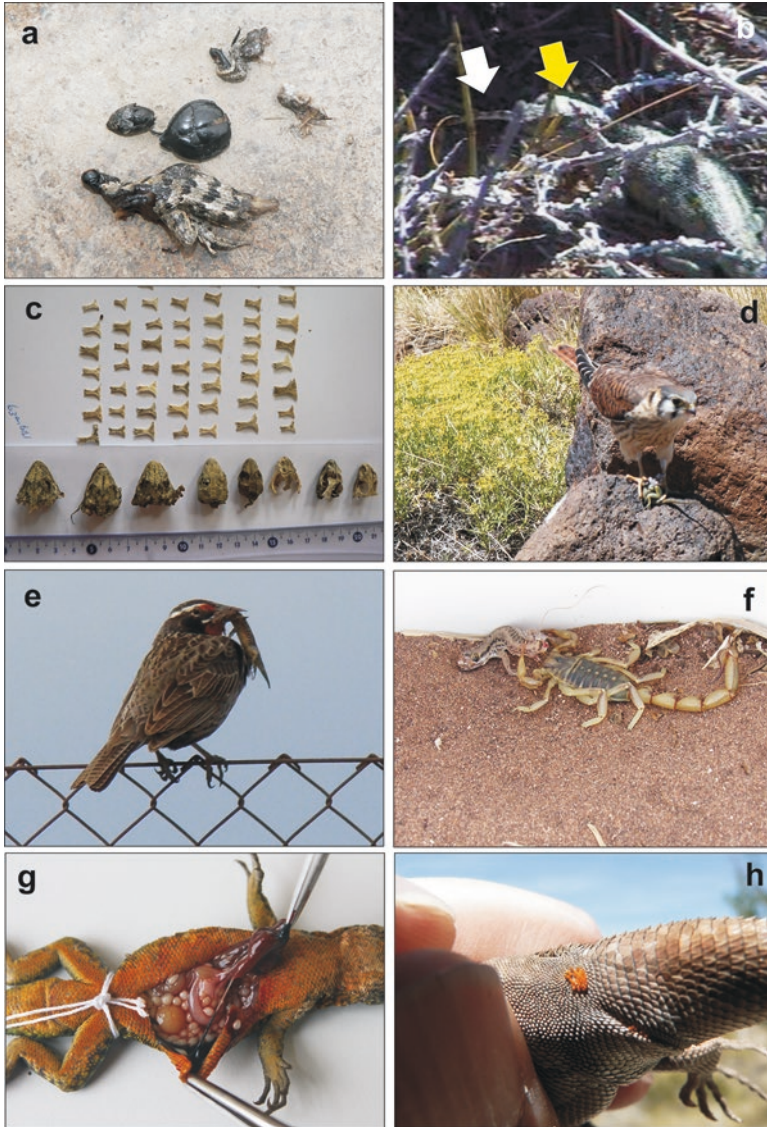
Several studies have emphasized the importance that omnivorous or herbivorous lizards have in the dispersal process, as fleshy fruits constitute a large part of their diets (Fellers and Drost 1991; Valido and Nogales 1994). Without doubt, *Phymaturus* species, saxicolous and herbivorous, are excellent potential seed dispersers. In the feces of *Phymaturus vociferator*, seeds from three species of plants are found: *Berberis empetrifolia*, *Rumex acetosella*, and *Calandrinia* sp. from the Laguna La Laja National Park in Chile. Studies carried out by Celedón-Neghme et al. (2005) demonstrate that *P. vociferator* has a clear preference for the consumption of *Calandrinia* sp., while at the same time the percentage of germination and viability for *B. empetrifolia* seeds is higher after having passed through the digestive tract. In addition, *P. vociferator* disperses seeds from the mother plant in an average area of

~20.75 m<sup>2</sup>, for which this lizard can be considered a legitimate disperser of these plants. Though there are no additional studies on the diet and seed dispersal of other *Phymaturus* species in Patagonia, it is likely that this numerous group of herbivorous lizards, together with other omnivorous and herbivorous *Liolaemus*, have a fundamental role as seed dispersers in the structure and diversity of vegetation in the Patagonia region, at least on a local scale in fragile Andean-Patagonian environments. Several *Phymaturus* species (*P. camilae*, *P. verdugo*) have been observed by the authors eating fruits of *Lycium* spp. (Fig. 11.3f) and *Berberis microphylla* (Pérez, personal communication), and it is common to observe some seeds in recent feces of species of this genus, but no studies on this issues have been carried out.

On the other hand, in Patagonia's natural systems, saurophagy is common in many large species, mainly lizards from the Leiosauridae family, among them *Diplolaemus darwini* (Pérez et al. 2009a) (Fig. 11.4a). Nevertheless, it has also been documented in *Liolaemus* species that coexist in sympatry, as is the case of syntopic *L. bibronii* with *L. petrophilus* and *L. austromendocinus*. They are often observed occupying the same microhabitats. For these last two species, juvenile and adult of *L. bibronii* have been reported as items of prey (Avila and Morando 2002; Pérez et al. 2009b). Another example is *Homonota underwoodi*, in whose stomach contents a juvenile of *L. darwini* was found (Blanco et al. 2012). Within saurophagy, cannibalism may also exist and in the majority of cases these predatory strategies appear as opportunistic and as a result of normal predatory behavior (Polis and Myers 1985). Reports of cannibalism exist for *Aurivela longicauda*, *Liolaemus rothi* (Fig. 11.4b), *L. darwini*, *L. chilensis*, *L. baguali*, and *Diplolaemus leopardinus* (Scolaro 2005; Pincheira-Donoso 2000; Ripoll and Acosta 2007; Kozykariski et al. 2009; Blanco et al. 2012).

Lizards are also part of interspecies predator-prey relationships with other groups of animals, where various lizards, among them *Liolaemus goetschi*, *L. lineomaculatus*, *L. fitzingerii*, *L. cyanogaster*, *L. chilensis*, *L. fuscus*, *Leiosaurus belli*, *Pristidactylus torquatus*, *Diplolaemus bibronii*, *Homonota darwini*, *H. underwoodi*, *Aurivela longicauda*, *Teius teyou*, and others, are often the prey of different predators such as birds (*Geranoaetus polyosoma* (common hawk), *Athene cunicularia* (burrowing owl) (Fig. 11.4c), *Bubo magellanicus* (Magellanic horned owl), *Falco sparverius* (American kestrel) (Fig. 11.4d), *Falco femoralis* (aplomado falcon), *Pseudoseisura gutturalis* (Cacholote), *Agriornis montana* (black-billed shrike-tyrant), and *Leistes loyca* (common meadowlark) (Fig. 11.4e)), snakes (*Philodryas chamissonis*, *Phylodrias psammophidea*, *Tachymenis chilensis*, *Bothrops ammodytoides*), and arachnids (*Lycosa polyostoma* (wolf spider), *Bothriurus burmeisteri*, *Tymogenes* sp. (scorpion) (Fig. 11.4f), and others (Greene 1992; Trejo et al. 2003; Figueroa Rojas et al. 2004; Pérez and Avila 2005; Udrizar Sauthier et al. 2007; Pérez et al. 2009a, b, 2010; Santillán et al. 2009; Avila and Pérez 2011; Bianchini 2014; Pérez and Minoli 2014; Avila et al. 2017; Galdeano et al. 2017; Gómez Alés et al. 2017a; Udrizar Sauthier et al. 2017)). As such, lizards are of utmost importance to trophic networks as essential components of ecosystem processes (Acosta et al. 2018) in the Patagonia region.





**Fig. 11.4** (a) Remain of a *Liolaemus* lizard hunted by a *Diplolaemus darwini* (courtesy of C.H.F. Pérez, Pérez et al. 2009a). (b) Cannibalism in *L. rothi* (courtesy of M. Kozykariski, Kozykariski et al. 2009). (c) Bone remains of *Leiosaurus belli* found around a burrowing owl (*Athene cunicularia*) nest (Udrizar Sauthier et al. 2007). (d) *Falco sparverius* eating a *Liolaemus elongatus* lizard in the Area Natural Protegida Tromen (courtesy of D. Paz Barreto). (e) *Leistes loyca* with a *L. multimaculatus* near El Condor Beach, Río Negro Province, Argentina (courtesy of M. Bianchini, Bianchini 2014). (f) *Tymogenes* spp. eating a *Homonota underwoodi* in the Bajo de Añelo, Neuquén, Argentina (courtesy of M.V. Brizio). (g) Unidentified internal parasites in *Liolaemus pictus*. (h) Thicks in femoral pocket in *L. austromendocinus*

## 11.4 Parasitism

Parasitism is one of the most common styles of life in the animal kingdom and is widespread within natural ecosystems (Castillo et al. 2018). Knowledge of parasitic relationships between hosts, such as lizards, and different types of parasites (mites, ticks, helminths, and nematodes, among others) is important both from an ecological point of view and in terms of host health, as these relationships can hinder important physiological processes, such as thermoregulation, digestion, and immune response (García-De la Peña et al. 2010; Vitt and Caldwell 2013; San Martín-Órdenes et al. 2019). Likewise, parasites are good ecological indicators and provide information on phylogenetic relationships with their hosts (Cruz Reyes 1993). Moreover, the alteration of habitats due to anthropic actions can generate physiological stress for some species, creating nutritional variations and the appearance of opportunistic parasite species. In this sense, the absence or presence of certain parasites can be indicators of host stress, which could reflect certain environmental changes (Brooks and McLennan 1991; Accattoli and Salazar Martínez 2012).

Negative effects that parasitism could cause include anemia and a decrease in performance, followed by a reduction in survival, competitiveness, thermoregulation, social interactions, the ability to attract mates, and, in the case of females, fertility (Vitt and Caldwell 2013). On the other hand, the presence of certain nematode endoparasites in the intestines of herbivorous lizards is common and is not necessarily a detrimental factor for the host, as these parasites can help with the decomposition of cellulose in the diets of these lizards (Jaksić and Fuentes 1980; Iverson 1982; Stevens and Hume 1998; Carothers and Jaksić 2001). Therefore, parasitism can be interpreted as a process of selection that affects the ecology, physiology, evolution, and life histories of its hosts (Vitt and Caldwell 2013).

The majority of works referring to parasitism in Argentina and Chile are limited to the description of species or isolated recordings of infestations (Table 11.2). Few studies aim to understand how a parasite can affect a host's survival or what its relationship is to body conditions, sex differences, or the existence of seasonal variations (climate and reproductive conditions), with respect to the prevalence and intensity of parasites on a given host (Juarez Heredia et al. 2014; Castillo et al. 2018). More specifically, reports of endoparasites and ectoparasites found on species of Patagonian lizards do exist (Table 11.2, Fig. 11.4g, h). In a recent review of reptile parasites in Chile, San Martín-Órdenes et al. (2019) report that *Liolaemus tenuis* is the species with the most diverse taxa of parasites registered (11 taxa and only three at species level) and that *Liolaemus chillanensis* has the highest number of identified species of parasites. Ecological or biological aspects resulting from the parasitic interaction have not been evaluated, as has been done for some non-Patagonian species.

For example, *Phymaturus extrilidus*, a species endemic to the Puna region, presents a greater intensity of nematodes in relation to a deficient body condition, greater environmental humidity, and to the monoxenic life cycle of the *Parapharyngodon riojensis* parasite (Castillo et al. 2018). As such, the average intensity of nematodes

**Table 11.2** List of lizard species and parasites registered in the Patagonia region, Argentina, and Chile

Host lizard	Parasites	References
<i>Salvator rufescens</i>	<i>Stryphlodora condita</i>	Lunaschi and Drago (2007)
<i>Pristidactylus torquatus</i>	<i>Eutrombicula araucanensis</i>	Stekol'nikov and González-Acuña (2015)
<i>Leiosaurus belli</i>	<i>Physaloptera retusa</i>	Goldberg et al. (2004)
<i>Liolaemus austromendocinus</i>	<i>Pterygosoma patagonica</i>	Dittmar De la Cruz et al. (2004)
<i>Liolaemus bibroni</i>	<i>Pterygosoma patagonica</i>	Dittmar De la Cruz et al. (2004)
<i>Liolaemus boulengeri</i>	<i>Parapharyngodon riojensis</i>	O'Grady and Dearing (2006)
<i>Liolaemus buergeri</i>	<i>Parapharyngodon riojensis</i>	Dittmar De la Cruz et al. (2004) and Goldberg et al. (2004)
	<i>Pterygosoma patagonica</i>	
<i>Liolaemus chiliensis</i>	<i>Spauligodon maytacapaci</i>	Goldberg et al. (2004) and San Martín-Órdenes et al. (2019)
	<i>Pterygosoma</i> sp.	
<i>Liolaemus chillanensis</i>	<i>Eutrombicula chillanensis</i>	Stekol'nikov and González-Acuña (2010, 2012, 2015) and Venzal et al. (2008)
	<i>Eutrombicula liolaemi</i>	
	<i>Microtrombicula mapuche</i>	
	<i>Morelacarus</i> sp.	
	<i>Ornithodoros rioplatensis</i>	
	<i>Parasecia molini</i>	
	<i>Paratrombicula chilensis</i>	
	<i>Paratrombicula goffi</i>	
<i>Liolaemus curicensis</i>	<i>Morelacarus</i> sp.	Stekol'nikov and González-Acuña (2015)
<i>Liolaemus cyanogaster</i>	<i>Pterygosoma cyanogasteri</i>	Fajfer and González-Acuña (2013)
<i>Liolaemus elongatus</i>	<i>Spauligodon maytacapaci</i>	Dittmar De la Cruz et al. (2004) and Goldberg et al. (2004)
	<i>Pterygosoma patagonica</i>	
<i>Liolaemus gracilis</i>	<i>Pterygosoma patagonica</i>	Dittmar De la Cruz et al. (2004)

(continued)

**Table 11.2** (continued)

Host lizard	Parasites	References
<i>Liolaemus lemniscatus</i>	<i>Eutrombicula araucanensis</i>	Goldberg et al. (2004) and Stekol'nikov and González-Acuña (2012, 2015)
	<i>Morelacarus</i> sp.	
	<i>Paratrombicula goffi</i>	
	<i>Spauligodon maytacapaci</i>	
	<i>Kiricephalus</i> sp. (nymphs)	
<i>Liolaemus monticola</i>	<i>Eutrombicula paula</i>	Stekol'nikov and González-Acuña (2010, 2015)
<i>Liolaemus neuquensis</i>	<i>Physaloptera retusa</i>	Goldberg et al. (2004)
<i>Liolaemus nitidus</i>	<i>Diaguitacarus choapensis</i>	Muñoz Leal (2013), Fajfer (2015) and Stekol'nikov and González-Acuña (2015)
	<i>Eutrombicula nerudai</i>	
	<i>Geckobia nitidus</i>	
	<i>Morelacarus</i> sp.	
	<i>Pterygosoma</i> sp.	
<i>Liolaemus petrophilus</i>	<i>Pterygosoma patagonica</i>	Dittmar De la Cruz et al. (2004)
<i>Liolaemus pictus</i>	<i>Eimeria liolaemi</i>	Daszak and Ball (1998), Espinoza-Carniglia et al. (2016), Fajfer and González-Acuña (2013), Goldberg et al. (2004) and Stekol'nikov and González-Acuña (2010)
	<i>Eutrombicula araucanensis</i>	
	<i>Pterygosoma</i> sp.	
	<i>Pterygosoma formosus</i>	
	<i>Pterygosoma levissima</i>	
	<i>Pterygosoma ligare</i>	
	<i>Pterygosoma ovata</i>	
	<i>Spauligodon maytacapaci</i>	
<i>Liolaemus rothi</i>	<i>Parapharyngodon riojensis</i>	O'Grady and Dearing (2006)
<i>Liolaemus septentrionalis</i>	<i>Eutrombicula araucanensis</i>	Stekol'nikov and González-Acuña (2010, 2015) and Espinoza-Carniglia et al. (2015, 2016)
	<i>Microtrombicula</i> sp.	
	<i>Morelacarus</i> sp.	
	<i>Parasecia</i> sp.	
<i>Liolaemus schroederi</i>	<i>Morelacarus</i> sp.	Stekol'nikov and González-Acuña (2015)

(continued)

**Table 11.2** (continued)

Host lizard	Parasites	References
<i>Liolaemus tenuis</i>	<i>Eutrombicula alfreddugesi</i>	Contreras et al. (1990), Daszak and Ball (1998), Goldberg et al. (2004), Rubio and Simonetti (2009) and Stekol'nikov and González-Acuña (2015)
	<i>Eutrombicula araucanensis</i>	
	<i>Eimeria liolaemi</i>	
	<i>Morelacarus</i> sp.	
	<i>Pharyngodon</i> sp.	
	<i>Pterygosma</i> sp.	
	<i>Spauligodon maytacapaci</i>	
	<i>Verversia</i> sp.	
<i>Phymaturus damasense</i>	<i>Parasecia molini</i>	Stekol'nikov and González-Acuña (2015)
<i>Phymaturus tenebrosus</i>	<i>Ornithodoros</i> sp.	Cabezas-Cartes et al. (2018b)
<i>Phymaturus vociferator</i>	<i>Eutrombicula chillanensis</i>	Venzal et al. (2008) and Marchant (2010)
	<i>Eutrombicula liolaemi</i>	
	<i>Ornithodoros rioplatensis</i>	
<i>Phymaturus zapalensis</i>	<i>Parapharyngodon riojensis</i>	O'Grady and Dearing (2006)

would be a good estimate to detect deficient physiological conditions of hosts (Castillo et al. 2018). Juárez Heredia et al. (2014) report ectoparasitic interaction between *Liolaemus pacha*, a species of lizard from northern Argentina which inhabits the Monte and Prepuna regions, and a mite of the genus *Pterygosoma*. These authors do not find seasonal variations with respect to mite intensity but do observe variation between sexes, with males having greater infestations than females. *Liolaemus pacha* males could be more exposed to ectoparasites as they have a greater “home range” than females (Halloy and Robles 2002), and on the other hand, hormonal imbalances of males during the reproductive season are generally associated with immune suppression, and as such, males are more susceptible to diseases or parasitosis (Salvador et al. 1996; Juárez Heredia et al. 2014). Carothers and Jaksić (2001) compared the distribution of ten *Liolaemus* species with the distribution of nematodes, ticks, mites, and the *Plasmodium* parasite with the objective of verifying if parasitism could be a determining factor for the limits of distribution of these lizards in the central Andes of Chile. These authors suggest that other interactions such as competition, predation, or environmental characteristics have a more predominant role in the altitudinal distribution of *Liolaemus* lizards, as opposed to parasitism. Jiménez (2005) compared the composition and magnitude of helminth parasites of three host populations of *Liolaemus tenuis* in Chile in order to assess whether the degree of environmental intervention is a determining factor in



parasitic communities. Results indicated that there were differences in composition and parasitic magnitude, which could be due to differences in the composition of the lizard assemblage, the population density of *L. tenuis*, and the history of colonization in the different sites (regions with few individuals would present a smaller pool of parasites and loss of intermediate hosts; Garín and González-Acuña 2008).

Detailed studies relating the intensity and prevalence of parasites on lizards with biological and environmental variables have not been carried out in the Patagonia region. For this reason, it is necessary to conduct studies that contribute to our understanding of the function that parasitism has as an important component of the region's ecological systems.

## 11.5 Resource Partitioning

A recurring question in ecological studies is why an assemblage of species exists in a certain area or how species with similar requirements interact and persist (Vitt and Caldwell 2013). One of the main answers to these questions is that available resources are limited and therefore an assemblage of species must divide these resources in order to survive. Consequently, lizard interactions such as competition, predation, and parasitism, among others, are mechanisms that determine which species will persist and which will not, at least for local assemblages (Pianka and Huey 1978; Vitt and Caldwell 2013). An assumption in ecology is that an assemblage's structure is strongly determined by interspecies competition, as resources such as food and space are limited (Pough et al. 2001). Competition for limited resources could determine how many species are able to coexist, what features they possess, and what different uses they make of these resources, under the assumption that segregation is what allows for coexistence (MacArthur 1972; Cody et al. 1975; Pough et al. 2001).

Resource partitioning between species within an assemblage is a mechanism that generally occurs in one or more principal niche aspects: space (microhabitat), activity time, and food, which is known as a complementary niche aspect (Schoener 1974; Pianka 1986). Moreover, competition and predation are not the only mechanisms which can lead to resource division, as other factors exist which operate independently of interspecific interactions, such as physiology, thermoregulation behavior, and morphological restrictions (Williams 1983; Pough et al. 2001), which could favor coexistence between sympatric species.

The diverse environments in Patagonia are home to numerous lizard assemblages, and it is likely that the coexistence of a highly diverse group of species is made possible, thanks to the partitioning of environmental resources. However, there are few integral studies of species' niche in the region that include temporal, spatial, and trophic interactions. Núñez (1996), for example, evaluated the use of time, space, and diet in the sympatric species *Liolaemus curis* and *L. curicensis* in Termas del Flaco, central Chile, in order to infer which factors intervene in their coexistence. Both species are saxicolous, but they occupy rocks of different sizes

and heights to sunbathe, which means they are not syntopic as they divide their microhabitat preferences. Nonetheless, spatial resource partitioning is not a competition mechanism but rather is due to intrinsic factors like body size and feeding, with a clear relationship existing between type of shelter and trophic offering provided by bushes. In terms of the temporal aspect, *L. curis* is bimodal while *L. curicensis* displays a unimodal pattern (active mainly in the morning). In this case, temporal segregation is determined by predator pressure and by different thermal requirements and behaviors of each species. The division of the thermal resource, determined by size and body mass, leads to a decrease in competitive interactions in other niche aspects, such as time and space (Barbault 1991; Pianka and Huey 1978; Gómez Alés et al. 2017b; Duran et al. 2018). Lastly, *L. curis* is an anteater while *L. curicensis* is a generalist in its feeding preferences. These differences are associated with the nutritional offering at the lizards' perch sites. As such, microhabitat use is the principal niche aspect allowing these species to coexist (Núñez 1996). On the other hand, Núñez et al. (1989) evaluated the degree of overlap between two syntopic species, *Liolaemus lemniscatus* and *L. fuscus*, in central Chile, considering three fundamental axes of the ecological niche (microhabitat, time, and food use) and incorporating seasonal variations. These authors found great similarities in the three dimensions of the niche during all seasons; the greatest overlap of microhabitat and time occurs during the seasons of abundant trophic resources (spring, summer), while during periods of food shortages (fall, winter) the overlap in diet and use of time is smaller (Núñez et al. 1989).

Conveying the importance of competition generally requires experimental manipulations in the field in order to be able to evaluate at a single site the use that a species in sympatry with another makes of resources in the absence of competition (Núñez et al. 1989). Nevertheless, though these situations are not frequent, they do occur naturally. In the Payunia region of southern Mendoza, Argentina, two *Phymaturus* species coexist in sympatry on volcanic rock. *Phymaturus roigorum* and *P. payuniaie* are herbivorous, viviparous lizards that can often be observed sunbathing on the same rocks and sharing shelters (Corbalán and Debandi 2013). Specifically, *P. roigorum* is found to be both in allopatry and syntopy with *P. payuniaie*, which represents an excellent natural scenario for evaluating the effect of competition on resource partitioning. Corbalán and Debandi (2014) demonstrated that for these strictly herbivorous species, diet segregation is the niche aspect that best explains their coexistence. Their foraging times are different (unimodal for *P. payuniaie* and bimodal for *P. roigorum*) at one of the sites where they are found in syntopy and where diet overlap is high. On the other hand, this study does not provide sufficient evidence to be able to conclude that competition among species is present in this system. *P. roigorum*'s activity and behavior patterns were not different at syntopy and allopatry sites, indicating that the presence of *P. payuniaie* has no influence (Corbalán and Debandi 2014). These authors present the hypothesis of habitat quality to explain the presence of larger *P. roigorum* males at syntopy sites and the absence of *P. payuniaie* at allopatric sites, due to the fact that sympatric sites have a greater proportion of adequate thermal microsites and food that these lizards prefer, such as *Fabiana punensis* and *Ephedra chilensis*, both absent at the allopatric sites.

Finally, intrinsic factors of life history such as body size, sex, or reproductive condition can help to minimize niche overlap in sympatry (Pianka 1973, 1986; Pough 1973; Vitt 2000; Pough et al. 2001), as has been observed, for example, in *Salvator rufescens*. This red iguana is widely distributed in the phytogeographical regions of the Monte and Chaco near the Patagonia region. In one of the Chaco sectors, this species is found to be in sympatry with *Salvator merianae*, and it has also been observed that body size, sexual maturity, and reproductive activity are relevant factors that influence diet (López Juri et al. 2015). As such, this is an example of how life history characteristics for these species influence diet composition and contribute to the coexistence of species by means of interspecific segregation of the trophic niche (López Juri et al. 2015). On the other hand, Cardozo et al. (2012) observed that these *Salvator* species differ in terms of habitat requirements when found in allopatry, while in the distribution contact zone they utilize the same habitat resources. Nevertheless, *S. rufescens* is associated with greater forest coverage, which could be determined by a trophic preference for native fruits and seeds (Cardozo et al. 2012).

## 11.6 Conclusions

There is abundant evidence to suggest that reptiles have entered into a process of biological diversity loss on a global scale due to human actions like habitat fragmentation and disturbances such as overgrazing, deforestation, forest clearing, expansion of agricultural borders, and global climate change (Acosta et al. 2018). Therefore, it is essential to deepen our knowledge of the diversity and ecology of this group as a fundamental step for its protection, conservation, and management. Throughout this chapter, we have been able to gather valuable information about Patagonian lizards regarding behavioral aspects and the use of trophic, temporal, and spatial resources, as well as its key role in the diverse Patagonian ecosystems (interspecific interactions). However, there are some challenges in filling information gaps that we have presented in each section. For example, knowledge about the role that parasitism can play in behavior, activity patterns, thermoregulation, and the survival of an organism is currently poor, although it should be included in any comprehensive strategy for reptile conservation.

To conclude, in a context of conservation of the diversity of Patagonian lizards and their environments, it is necessary to be aware of diverse biological and ecological parameters. In this sense, the analysis of the abundance of species is of utmost importance and is essential to evaluating seasonal and annual variations in different populations. There are few studies that seek to measure the population density of Patagonian lizards. This negatively affects conservation measures needed in the face of ever-increasing human activity, which compromises both environments and their species. Although this is a daunting task, we challenge researchers to continue publishing on diverse aspects of lizard ecology with special emphasis on long-term studies that evaluate the population dynamics of the species.

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